Plant growth-form and climate controls on production and decomposition in northern peatlands

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PLANT GROWTH-FORM AND CLIMATE CONTROLS ON PRODUCTION AND DECOMPOSITION IN NORTHERN PEATLANDS

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CHAPTER 1

GENERAL INTRODUCTION

CLIMATE CHANGE AND THE CARBON BALANCE OF NORTHERN PEATLANDS

Northern peatlands cover large parts of arctic, sub-arctic and boreal regions (Gorham 1991, Houghton et al. 2001). They play an important role in the global carbon balance as a long-term carbon sink, because of a greater carbon sequestration through plant production than carbon release through decomposition of dead, organic tissues. Peatlands are estimated to be responsible for 5 % of the global net carbon flux from atmosphere to land (Houghton et al. 2001). As a result, one-third of the total world soil carbon pool has accumulated in peatlands over the past millennia, as thick layers of partly decomposed dead plant material (Gorham 1991).

The carbon dynamics of northern peatlands are strongly controlled by low temperatures and nutrient inputs, and usually high soil moisture contents (Aerts et al. 1992, Shaver et al. 1992, Johnson & Damman 1993, Updegraff et al. 2001). However, pronounced changes in the climate at northern high latitudes are expected for the 21st

century, as a consequence of increased concentrations of greenhouse gases (CO_2, CH_4, N_2O) in the atmosphere (Houghton et al. 2001). Predicted changes in climatic conditions in these regions include higher summer and winter temperatures, changes in the thickness and duration of the winter snow cover and in the amount of summer precipitation, and a longer growing season (Maxwell et al. 1992, Houghton et al. 2001, McCarthy et al. 2001). Such changes in climate may stimulate both organic matter production and decay rates. However, despite the importance as a feedback to the global carbon balance and climate itself, the magnitude and even the sign of the net effect of climate change on the carbon balance of northern peatlands remain unclear (Shaver et al. 2000, Hobbie et al. 2000).

Predicting the net effects of climate change on the carbon balance of peatlands is complex, because the processes of uptake and release of CO_2 by natural ecosystems are not independent. As a result of photosynthesis and biomass production by plants, subsequent senescence of their tissues, and the heterotrophic decomposition and mineralisation of the dead organic materials by soil fauna and microbes, carbon cycles in fact through the different compartments of ecosystems and the atmosphere (Fig. 1). Furthermore, the carbon cycle strongly interacts with the cycles of other elements, particularly nitrogen (N) and phosphorus (P). These nutrients, together with carbon, are essential constituents of plant tissues, and plants therefore depend on their availability for growth. However, inputs from external sources, such as precipitation or microbial N-fixation, or from weathering of mineral soil, are limited in northern peatlands or inaccessible due to the thick peat layers or permafrost. Recycling of the large pools of organically bound nutrients in the accumulated dead plant remains, through decomposition and mineralisation, is therefore a primary nutrient source for plant growth in northern peatlands (Rosswall & Granhall 1980, Malmer & Nihlgård 1980, Shaver et al. 1992).

At present, the slow decay rates in peatlands strongly constrain plant production, but climate warming and enhanced precipitation may change this. Temperature and moisture are key regulators of many biological processes, and are likely to affect most of the above-mentioned carbon and nutrient cycling processes, and their interactions. The net effect of climate change on the long-term carbon balance of peatlands will thus not only depend on the direct responses of plant production and decomposition, but also on indirect feedbacks, via interactions between carbon and nutrient dynamics (Shaver et al. 2000).

CLIMATE CHANGE AND PLANT PRODUCTION IN NORTHERN PEATLANDS

Responses of plant biomass production to climate change in the arctic have received considerable research attention during the last decades, especially in whole-ecosystem level manipulations of growing season temperatures or nutrient availability, which is likely

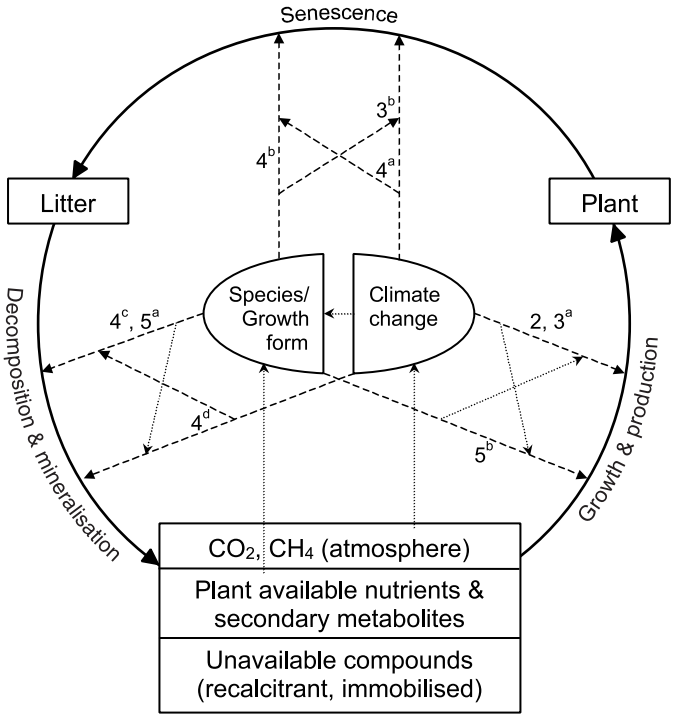

Fig. 1 Schematic representation of the main potential direct and plant-species mediated effects of climate change (dashed and dotted arrows) on carbon and nutrient cycling through peatlands. Climate change may, directly or via shifts in species or growth-form abundance, affect both the magnitude and the chemical composition of the fluxes (solid arrows) and pools (blocks) of carbon and nutrients. Climate change may also interact with the species/growth-form controls on these fluxes, and *vice versa*. Dashed arrows, with numbers, indicate relations and interactions investigated in the respective chapters of this thesis. For further explanation of the diagram, see text.

to increase upon warming (e.g. Chapin & Shaver 1985, Parsons et al. 1994, Jonasson et al. 1999, Arft et al. 1999, Rustad et al. 2001). Meta-analyses of the results of 9-20 of these experiments showed that, overall, higher temperatures, but especially enhanced nutrient availability, indeed stimulated the growth and biomass production of the whole vegetation (Arft et al. 1999, Rustad et al. 2001, Dormann & Woodin 2002, Van Wijk et al. 2003). However, the results were highly variable among the experiments, because of differences in the experimental methods and duration of the studies, and because of differences among the species compositions of the vegetation of the sites.

Plant species clearly differ in their responses to changes in temperature and nutrient availability, as a result of differences in inherent phenotypic plasticity of their growth, morphology, and nutrient uptake (Parsons et al. 1994, Chapin & Shaver 1996, Bret-Harte et al. 2001). Changes in climate and nutrient availability may therefore alter the biomass

and structure of the vegetation directly, but also indirectly through changing competitive interactions (Harte & Shaw 1995, Press et al. 1998, Cornelissen et al. 2001, Weltzin et al. 2003), ultimately resulting in shifts in species composition. The species composition and the structure of the vegetation are thus important indicators of potential long-term climate-change effects on plant production and carbon sequestration (Fig. 1).

The vascular vegetation of northern peatlands, like that of several other nutrient-limited ecosystems, is dominated by woody and rhizomatous perennials, including many ericaceous dwarf shrubs (such as *Andromeda polifolia*, *Vaccinium* spp., *Empetrum nigrum*) and other dwarf shrubs (*Betula nana*, *Salix* spp.), and a range of grasses (notably *Calamagrostis* spp.) and sedges (*Rhynchospora* spp., *Carex* spp., *Eriophorum* spp.) (Clymo & Hayward 1982, Backéus 1985, Rydin et al. 1999). However, it stands out from that of many other ecosystems by the great abundance of mosses, especially peat mosses (*Sphagnum* spp.). Particularly in ombrotrophic bogs, dense *Sphagnum* carpets may dominate the vegetation. Their great abundance may have important consequences for the responses of peatlands to climate change. In bryophyte-rich ecosystems, such as bogs, mosses may also account for the majority of the biomass production (Oechel & Van Cleve 1986, Weltzin et al. 2000). *Sphagnum* mosses differ fundamentally from other plants in their morphology, physiology and chemistry (Clymo & Hayward 1982, Van Breemen 1995, Verhoeven & Liefveld 1997), and their responses to climate change may therefore differ from that of vascular plants. *Sphagnum* plants lack roots and an internal vascular system for water and solute transport, and have only a limited cuticle. *Sphagnum* accumulates water passively in the porose hyaline cells of the living and dead tissues, and in the capillary spaces between the stems and branches, which keeps the water content of peatlands generally high. Furthermore, these mosses absorb nutrients with their entire surface, not only from below, but also directly from the precipitation on top of their shoots (Malmer 1993). These properties make *Sphagnum* plants far more sensitive to drought than vascular plants in peatlands, but less dependent on the recycling of nutrients from organic matter.

Sphagnum properties may also affect the growth and production of the vascular plants in northern peatlands, and may interfere with their responses to climate change. *Sphagnum* mosses strongly reduce the availability of nutrients in the rooting zone of vascular plants, through their efficient absorption of nutrients and through inhibition of decomposition by creating cold, anoxic, acid conditions (Clymo & Hayward 1982, Johnson & Damman 1993, Malmer et al. 1994). Although mosses occupy the bottom layer of the vegetation, they may thus be effective competitors to vascular plants, whose survival is continuously threatened by the progressively increasing height of the *Sphagnum* carpet in which they grow (Oechel & Van Cleve 1986, Backéus 1985, Malmer et al. 1994, Van Breemen et al. 1995). Changes in environmental conditions may alter these competitive interactions because of different

growth and production responses of *Sphagnum* and vascular plants, as has been shown in relation to increased atmospheric N-deposition, another important component of global change (Berendse et al. 2001, Limpens et al. 2003). However, the effects of the expected changes in the climate of high-latitude regions on the production of *Sphagnum* mosses, and on their interactions with vascular plants, have been largely overlooked so far. In this thesis, I will therefore focus on these topics in the chapters 2 and 3 (Fig. 1, relations 2 and 3, interaction 3b).

CLIMATE CHANGE AND DECOMPOSITION IN NORTHERN PEATLANDS

The decomposition of dead tissues (litter) is controlled by three main factors: the climate, the chemical and physical properties of the litter (litter quality), and the composition and abundance of the decomposer community (Swift et al. 1979). The most important climatic variables are temperature and moisture availability, which directly affect the activity of soil microorganisms and their catalytic enzymes, as well as physical processes related to decomposition (leaching, freeze-thaw action). At a global scale, the decomposition rate of litter is therefore strongly related to the actual evapotranspiration (AET), an index that integrates both climatic factors (Meentemeyer 1978, Aerts 1997). In experimental warming studies, increases in soil temperature have been shown to strongly stimulate soil respiration and N-mineralisation (Nadelhoffer et al. 1991, Rustad et al. 2001). Decomposition of fresh litter and associated N-losses may also be stimulated by higher temperatures, depending on the species and moisture conditions (Hobbie 1996, Robinson et al. 1995, Shaw & Harte 2001). Climate warming and increased precipitation may thus directly enhance the release of carbon and nutrients from the organic matter in northern peatlands.

In the longer-term, however, indirect climate-change effects, via phenotypic or interspecific changes in the quality of new litter, may become at least as important, because fast depletion of the labile soil carbon pool and the low chemical quality of the remaining organic material may restrict further direct effects of warming on soil respiration (Christensen et al. 1999, Rustad et al. 2001). Decomposition has since long been related to a wide range of chemical and physical properties of the litter (e.g. Waksman & Tenney 1928, Coulson & Butterfield 1978, Melillo et al. 1982, Verhoeven & Toth 1995, Cornelissen et al. 1999). Decomposer organisms use dead tissues as a source of carbon and nutrients for growth, and as an energy source. The relative amounts of carbon and nutrients contained in organic molecules, as well as their energy content and accessibility for enzymes, are thus important indicators of litter decomposability (Swift et al. 1979). At a regional scale, litter decomposition has therefore most successfully been related to the total concentrations of several elements (carbon, N and P), concentrations of specific groups of organic

compounds (lignin, (hemi)cellulose, phenolics), and particularly to various ratios of these concentrations (lignin/N, C/N, phenol/N, phenol/P) (Melillo et al. 1982, Hobbie 1996, Aerts & Chapin 2000).

Plant species differ widely in the chemical and physical properties of the litter they produce, and therefore in litter decomposability (Coulson & Butterfield 1978, Swift et al. 1979, Hobbie 1996, Aerts & Chapin 2000, Pérez-Harguindeguy et al. 2000). Changes in temperature and precipitation, and associated increases in nutrient availability, may alter the overall quality and decomposability of the litter input of ecosystems, by affecting the litter properties of individual plant species (Shaw & Harte 2001, Van Heerwaarden et al. 2003), as well as the species composition of the vegetation (Harte & Shaw 1995, Press et al. 1998, Weltzin et al. 2003). Such plant-mediated changes may be at least as important for carbon and nutrient cycling as direct climate effects (Hobbie 1996, Hobbie et al. 2000, Shaver et al. 2000). Differences and patterns among groups of plant species in their effects on litter quality, decomposability, and the feedbacks of their decomposing litters to plant production, through release of nutrients and other plant available compounds, will be the focus of the chapters 4 and 5 of this thesis (Fig. 1, relations 4 and 5).

PLANT GROWTH FORMS AS A FUNCTIONAL CLASSIFICATION

As indicated in the previous sections, differences among plant species in their responses to climate change, and in their effects on carbon and nutrient cycling processes, may play a key role in the feedback of northern peatlands to the global carbon balance. However, the vast areas of these peatlands differ substantially in the species composition of their plant community (Backéus 1985, Rydin et al. 1999, Berendse et al. 2001). To understand the controls of different plants on carbon and nutrient cycling, and to predict ecosystem responses to climate change on a global scale, we thus need to generalise plant responses and effects, by grouping species into a limited number of 'plant functional types' (Chapin et al. 1996, Gitay & Noble 1997). Plant functional types are groups of plant species that show a similar response to variation in environmental conditions, or have a similar effect on ecosystem processes (Gitay & Noble 1997, Lavorel et al. 1997).

A range of plant characteristics have been put forward to serve as classifying criteria, or to use as predictors of plant responses to their environment or their impacts on ecosystem processes (e.g. Aerts 1995, Chapin et al. 1996, Cornelissen 1996, Lavorel et al. 1997, Poorter 1998, Grime 2001, Lavorel & Garnier 2002). The applicability of those characteristics is, however, often limited to a certain type of environmental disturbance or constraint, or a small number of specific ecological processes, or to relatively few species because their classification involves elaborate measurements. Climate change affects

the carbon balance of northern peatlands via multiple, interdependent environmental factors (temperature, moisture, nutrient availability). Plant feedbacks to the carbon and nutrient cycles involve both differences in production responses to these environmental disturbances, and differences in their effects on decomposition and nutrient mineralisation processes. Ideally, one single functional type classification of species should thus allow for easy classification of the species, and be able to describe both responses to, and effects on, these multiple environmental factors and ecosystem processes.

In arctic research, plant growth forms have been used widely to describe the distribution of plants across natural gradients and their responses to experimental manipulations of environmental conditions (e.g. Chapin et al. 1995, Shaver et al. 1996, Arft et al. 1999, Dormann & Woodin 2002, Van Wijk et al. 2003). Growth forms represent subjectively defined groups, differing in size, morphology and life-span characteristics, such as the presence of a vascular system or supportive (woody) tissues, and the shape, structure and longevity of leaves (Fig. 2). These characteristics may have important consequences for their functioning, by affecting their growth potential, nutrient dynamics, defence of tissues, and competitive ability. Cluster analysis of plant species differing in a range of plant characteristics related to responses to climate and disturbance, resource acquisition, nutrient use and competitive ability, supported the functional homogeneity of the growth forms, and their potential as a functional classification for climate change studies in cold, northern biomes (Chapin et al. 1996).

So far, the results of environment manipulation studies have indicated that growth forms may indeed differ in their production and biomass responses to increased temperatures, and nutrient and moisture availability (Chapin et al. 1995, Dormann &

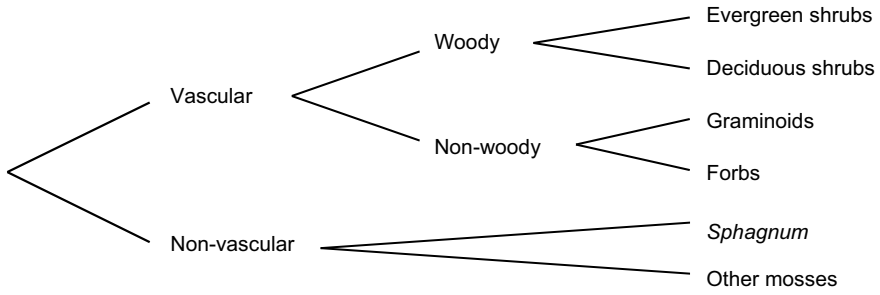

Fig. 2 Simplified plant functional type classification for cold, northern biomes based on plant growth forms, whose responses to climate change and effects on carbon and nutrient cycling may differ because of the functional consequences of their morphology (adapted from Chapin et al. 1996). Graminoids include grasses, sedges and rushes; forbs include herbaceous dicots.

Woodin 2002, Van Wijk et al. 2003), although the differences may vary among vegetation types and ecosystems. In chapters 2 and 3, we will therefore include species of different growth forms to investigate their growth and production responses to year-round climate change in a sub-arctic bog.

Broad screenings of species from a range of natural ecosystems have shown that growth forms may also differ in their litter quality and decomposability (Cornelissen 1996, Aerts & Chapin 2000, Pérez-Harguindeguy et al. 2000). Direct comparisons among a range of growth forms in their litter effects on nutrient release and plant growth have not yet been performed. However, their applicability as predictors of plant-mediated climate-change effects on ecosystem processes, such as decomposition and nutrient mineralisation, requires that growth forms do not only differ under current climatic conditions, but the differences and patterns need to hold under changed conditions as well (Gitay & Noble 1997, Lavorel et al. 1997). So far, it remains uncertain how species-specific responses of litter quality and decomposability to climate change (Hobbie 1996, Shaw & Harte 2001) will affect the homogeneity within, and differences among, the growth forms in their effects on ecosystem processes. The reliability of a growth-form based classification for predicting plant-mediated climate change effects on litter chemistry, decomposability, and litter feedbacks to plant growth will therefore be further investigated in the chapters 4 and 5 (Fig. 1, interactions 4a and 4d, relations 5a and 5b).

AIMS AND OUTLINE OF THIS THESIS

The general aim of this thesis is to investigate how climate change will alter key components of the carbon cycle of northern peatlands, and particularly whether plant growth-form based functional classifications provide a useful tool to generalise plant-mediated responses and effects. The complete responses of the carbon cycle involve a large number of processes and feedbacks, which may take a range of shorter and longer time scales to evolve and to reach equilibrium in natural ecosystems (Shaver et al. 2000). A comprehensive investigation of all processes and feedbacks is therefore far beyond the scope of this thesis. Instead have I restricted myself to several of the key uncertainties, introduced in the previous sections, that will increase our understanding of climate and plant growth-form controls on the carbon and nutrient dynamics of northern peatlands. The two main questions for the following chapters of this thesis are therefore: (1) What are the effects of changes in summer and winter climate on growth and production of species of different plant growth forms, including *Sphagnum*, in northern peatlands? (2) Can we use plant growth forms to generalise inter-specific differences in litter-decomposition feedbacks to climate change? These overall questions were investigated in three separate experiments, of which the explicit hypotheses and

results are introduced and discussed in the following four chapters. The general outline of this thesis, and the approach of the questions, is as follows.

Question (1) was investigated in an ecosystem-level experiment in a sub-arctic blanket-bog in north Sweden, in which we manipulated summer temperatures, winter snow-cover thickness, and spring temperatures, in six different combinations. The experiment is introduced and the effects of the manipulations on the microclimate are discussed in **chapter 2**. Furthermore, in this chapter we answer the question how such changes in climate directly affect the growth, carpet structure and biomass production of the dominant moss, *Sphagnum fuscum* (Fig. 1, relation 2). Subsequently, in **chapter 3** we investigate whether direct and *Sphagnum*-mediated effects of the applied changes in summer, winter and spring climate have the potential to affect the survival and performance of four vascular plant species representing different growth forms, through changes in their length growth and leaf litter production (Fig. 1, relation 3a and relation/interaction 3b).

Several aspects of question (2) were investigated in two separate experiments, which are the focus of the second half of this thesis. In **chapter 4**, we report whether plant growth forms are consistent, environment-independent predictors of leaf litter chemistry and decomposability in peatlands. We used the variation in environmental conditions (temperature, precipitation, N-deposition) along a large-scale, latitudinal gradient in north-west Europe, and investigated the consistency of the patterns of a range of litter chemistry variables and decomposability among five growth forms along this environmental gradient (Fig. 1, interactions 4a and 4d). Moreover, the relative importance of environmental conditions and growth forms as controls on litter chemistry and decomposability were compared (Fig. 1, relations 4a and 4b, 4c and 4d), as well as the ability of growth forms and traditional, bulk litter chemistry indices to predict differences in litter decomposition. The cycles of nutrients and carbon through plants and litter is completed in **chapter 5**, in which we investigate whether leaf-litter feedbacks to new plant production differ among growth forms, and how such differences are related to their litter chemistry and decomposability (Fig. 1, relations 5a and 5b). These questions were addressed in a phyto-assay, by comparing the production responses of a potted test plant to decomposing leaf litters of a range of 20 sub-arctic, vascular peatland species of contrasting growth forms.

Finally, in **chapter 6**, the most important results of the respective chapters are integrated with complementary literature, in an attempt to answer the general question whether plant growth-form based classifications are useful in predicting ecosystem feedbacks to climate change.

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CHAPTER 2

SUMMER WARMING AND INCREASED WINTER SNOW COVER AFFECT *SPHAGNUM FUSCUM* GROWTH, STRUCTURE AND PRODUCTION IN A SUB-ARCTIC BOG

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ABSTRACT

Sphagnum mosses form a major component of northern peatlands, which are expected to experience substantially higher increases in temperature and winter precipitation than the global average. *Sphagnum* may play an important role in the responses of the global carbon cycle to climate change. We investigated the responses of summer length growth, carpet structure and production in *Sphagnum fuscum* to experimentally induced changes in climate in a sub-arctic bog. Thereto, we used open-top chambers (OTCs) to create six climate scenarios including changes in summer temperatures, and changes in winter snow cover and spring temperatures. In winter the OTCs doubled the snow thickness, resulting in 0.5-2.8 °C higher average air temperatures. Spring air temperatures in OTCs increased by 1.0 °C. Summer warming had a maximum effect of 0.9 °C, while vapor pressure deficit was not affected. The climate manipulations had strong effects on *S. fuscum*. Summer warming enhanced the length increment by 42-62 %, whereas bulk density decreased.

This resulted in a trend ($P < 0.10$) of enhanced biomass production. Winter snow addition enhanced dry matter production by 33 %, despite the fact that length growth and bulk density did not change significantly. The addition of spring warming to snow addition alone did not significantly enhance this effect, but we may have missed part of the early spring growth. There were no interactions between the manipulations in summer and those in winter/spring, indicating that the effects were additive. Summer warming may in the long term negatively affect productivity through the adverse effects of changes in *Sphagnum* structure on moisture holding and transporting capacity. Moreover, the strong length growth enhancement may affect interactions with other mosses and vascular plants. Because winter snow addition enhanced the production of *S. fuscum* without affecting its structure, it may increase the carbon balance of northern peatlands.

INTRODUCTION

Sphagnum mosses form a major component of sub-arctic and boreal peatlands, which cover 2 % of the total land area (Gorham, 1991; Houghton *et al*., 2001). These peatlands have acted as a long-term net carbon sink and take up 0.07 Pg carbon per year (Gorham, 1991; Clymo *et al*., 1998), equivalent to 5 % of the total net carbon flux from atmosphere to land (Houghton *et al*., 2001). Arctic and sub-arctic areas are very likely to experience increases in temperature and winter precipitation above the global average during the upcoming century (Houghton *et al*., 2001). Climatic conditions are important regulators of ecological processes, while changes in the uptake and release of carbon in northern peatlands can also have major feedback effects on climate itself. Over the past millennia, approximately one-third of the total world soil carbon has accumulated in the organic deposits of those peatlands (Gorham, 1991), mainly due to the recalcitrant nature of *Sphagnum* litter and the unfavorable conditions for decomposition, such as low temperatures, low pH and a high water table (Johnson & Damman, 1993). *Sphagnum* mosses have thus been responsible for the sequestration of large quantities of carbon and play an important role in the global carbon cycle. Climate change is likely to alter the accumulation of carbon by *Sphagnum*, with consequences for the sink function of northern peatlands.

The accumulation of organic carbon is the result of production and decay of *Sphagnum* tissues. Increasing soil temperatures may directly enhance decomposition processes (Rosswall *et al*., 1975, Hobbie, 1996), which could result in a positive climatic feedback by increasing atmospheric CO_2 and CH_4 concentrations (Updegraff *et al*., 2001). Increased snow cover has been reported to have similar but weaker effects on greenhouse gas emissions, both through its direct effect on winter soil temperatures and, in combination with summer warming, by improving the soil moisture conditions (Jones *et al*., 1998). Much

less is known about the effects of climate change on productivity (organic matter fixed per unit time). It has been suggested that climate warming may stimulate plant productivity, resulting in a higher carbon uptake (Gorham, 1991; Tenhunen *et al*., 1992). *Sphagnum* productivity is indeed higher at lower latitudes (Wieder & Lang, 1983), and is positively related to mean annual temperatures (Moore, 1989), indicating a climatic control. Increased summer temperatures in field and mesocosm experiments, however, either did not affect *Sphagnum* biomass or showed a reduction in the production (specific mass produced over a specific time interval; Hobbie & Chapin, 1998; Hobbie *et al*., 1999; Weltzin *et al*., 2001), possibly because of dehydration during the experiments. Higher evapotranspiration may be a result of a warmer climate, and lead to less favorable conditions for *Sphagnum* production (Skre & Oechel, 1981; Silvola & Aaltonen, 1984; Tenhunen *et al*., 1992). Changes in the climatic conditions outside the growing season, however, may also affect the productivity of *Sphagnum*, but so far this has not been investigated. A thicker snow cover in winter may protect the capitula against frost damage and frost drought, resulting in a higher production during the subsequent summer. Moreover, the increased amount of winter precipitation can be expected to result in higher soil moisture contents at least during the beginning of the subsequent growing season (Maxwell, 1992). Recent warming in the arctic shows that late-winter and early-spring temperatures may increase even more than summer temperatures (McCarthy *et al.*, 2001). Even in combination with an increased snow cover, such early warming is expected to result in an earlier onset of the growing season (Maxwell, 1992). Spring warming, in addition to the higher soil moisture conditions after melting of the increased snow cover, may therefore further enhance *Sphagnum* productivity.

In the longer term, climate change may alter the carbon balance of peatlands through changes in *Sphagnum* length growth and carpet structure. Changes in the structure of the *Sphagnum* carpet, due to different responses in length growth and productivity, may directly affect the thermal and hydrological regime in the peat (Williams & Smith, 1989), with feedbacks to both production and decay processes. Changes in climatic conditions may also affect competition among bryophytes, both through direct moisture changes and through the effects on *Sphagnum* density and growth rate (Rydin, 1997; Sonesson *et al*., 2002). These changes in *Sphagnum* performance may also affect the relation between *Sphagnum* mosses and higher plants (Malmer *et al*., 1994). This may have important consequences for the long-term stability of the *Sphagnum* dominated community.

In this study, we investigated the field responses of *Sphagnum fuscum* (Schimp.) H. Klinggr. to changes in summer and winter climate. In a sub-arctic blanket bog in north Sweden, we manipulated both summer temperatures and winter snow cover and spring temperatures, in factorial combinations. Here, we report the effects of the resulting six climate change scenarios on environmental parameters and *Sphagnum* performance in

the second and third years of the experiment. We focussed on *Sphagnum* length growth and carpet structure as well as on biomass production in the summer, and tested the following hypotheses. (I) Increased summer temperatures will have a minor effect on *Sphagnum* length growth and production, because of the counteracting effects of warming and increased evapotranspiration. (II) A thicker snow layer in winter will stimulate the production, by protecting the capitula and increasing the soil moisture. The latter factor may also positively affect length increment. (III) Higher spring temperatures, together with increased snow cover, will further enhance production and length growth by combining the positive effects of warming, higher soil moisture and snow protection.

MATERIALS AND METHODS

Experimental design

The climate manipulation experiment was established on a slightly sloping bog on the southern shore of Lake Torneträsk, Abisko, Sweden (68°21'N, 18°49'E). The vegetation is dominated by a continuous and homogeneous *S. fuscum* layer. Other bryophytes and lichens are sparse. The vascular plant community is low and open, and consists mainly of *Empetrum hermaphroditum*, *Rubus chamaemorus* and *Andromeda polifolia*. The distance to the water table increases along the slope upward from approximately -20 to -40 cm (July 2001). Permafrost is present at a depth of approximately -45 cm.

In June 2000, 30 plots were laid out on the bog at a minimal distance of 2 m. The site was divided into five blocks, perpendicular to the direction of the slope. Each block contained six plots, which were randomly assigned to one of the six climate change treatments. The climate manipulations were full factorial combinations of two summer treatments (ambient, warming) and three winter treatments (ambient, snow addition, snow addition plus spring warming) (see Table 1). The summer manipulations lasted from the first week of June until the last week of September. During this period, air and soil temperatures in the warming plots were passively increased by placing hexagonal ITEX open-top chambers (OTCs) over the vegetation (Marion *et al*., 1997). The chambers were 50 cm high, had a diameter of 1.6-1.8 m at the top and 2.2-2.5 m at the bottom, and were made of transparent polycarbonate (Makro life, Arlaplast, Sweden). Outside the growing season, we simulated three winter climate scenarios, which consisted of manipulations during two distinct periods. From the last week of September until mid-April, OTCs were placed on the snow addition and snow addition plus spring warming plots. Because of the exposed position of the site to the wind, the ambient snow cover was generally shallow. Inside the OTCs, however, snow passively accumulated during winters. In the second half of April, after most of the snow had melted,

Table 1 Experimental design and treatment codes used for the climate manipulations

	Summer treatment	
Winter treatment	Ambient	Warming
Ambient	AA	WA
Snow addition	AS	WS
Snow addition plus spring warming	AS +	WS +

the OTCs were removed from the snow accumulation plots. At the same time, excess snow (compared with ambient plots) was removed from these plots, to prevent carry-over effects of the winter treatment on the early-spring temperatures and freeze-thaw cycles. In May, the snow addition plus spring warming plots were thus the only ones with OTCs.

Environmental parameters

Air temperature at 5 cm above the *Sphagnum* surface and soil temperature at 5 cm below the surface were recorded continuously and averaged over 2-h intervals for all treatments in three of the five blocks, using NTC thermistor probes and dataloggers (Axiom SmartReader Plus 8). The air probes were covered by shade caps, which allowed free airflow around the probe. Snow cover in the center of each plot was measured weekly during the winter season using a wooden gauge. During the third summer season (2002), the effect of the manipulations on the vapor pressure deficit (VPD) was measured in the period of strongest *Sphagnum* growth. Thereto, we recorded the relative air humidity and air temperature at 5 cm above the *Sphagnum* carpet five times in June and July in the center of each plot during 5 min, using a hand-held humidity temperature datalogger (Center 314). The data were averaged over the 5-min intervals for each plot and used to calculate VPD (Rosenberg *et al*., 1983).

Sphagnum *measurements*

S. fuscum length increment was measured at five positions in the central part of each plot, using a modification of the cranked wire method (Clymo, 1970). Straight stainless wires (15 cm long) with a ring of short bristles at the lower end were inserted ca. 10 cm into the *Sphagnum* carpet. We avoided positions overgrown by other plants. We followed the length growth between 8 June and 27 September 2001, and between 28 May and 1 October 2002 by regularly recording the height of the wire top above the *Sphagnum* capitula, using a thin glass tube with a millimeter scale. The wires were left in place during the winter, but because we could not control for possible movements due to freezing and thawing, we did not include the changes in the height of the wires during the winter into the growth

calculations. The measurements for the five wires within each plot were averaged before the statistical analyses.

After the last length increment recording on 1 October 2002, we took 3-cm deep *Sphagnum* samples in a fixed area around four of the five wires in each plot, using a soil corer with an inside diameter of 2.8 cm. One of the wires was located in the nondestructive part of each plot and therefore could not be harvested. Each sample was cut into three layers. The upper part of 0.5 cm (containing the capitula) and the next part from 0.5 to 1.5 cm were oven dried at 60°C for 48 h and weighed to determine the capitulum bulk density and the subcapitulum bulk density, respectively. The rest of the sample was not used, since it might have been produced before the experimental manipulation, especially in the plots with the lowest length increment. The total production was calculated for each of the two summers by multiplying the length increment and the subcapitulum bulk density.

Statistical analyses

To compare the general effects of the manipulations on climatic parameters during the 2 years of our study, we calculated daily average, minimum and maximum temperatures and averaged those over five climatically different periods within each year (October-January, February-April, late April-May, June-July and August-September). Snow depth data were averaged over the same periods in winter. For a more detailed analysis of the air and soil temperature data and the snow data of the first year (September 2000-August 2001) in shorter periods we refer to Aerts *et al.* (unpublished results). Repeated-measures multivariate ANOVAS (Pillai's trace) were used to analyze the effects of the treatments on temperature parameters and snow thickness, with year as the within-subject factor and summer treatment and winter treatment as the between-subject factors. The analyses were performed for each sub-season separately, where the spring warming period (late-April-May) was considered as a separate sub-season during the winter manipulations. At first, the data of all periods within a sub-season (winter, spring or summer) for both years were included in the same analysis. If significant interactions of year and summer treatment, year and winter treatment or year and summer × winter treatment were found, the analysis was repeated for the two periods within a sub-season separately, but for combined years. Only if the interactions with year were still significant did we split the data into separate years and performed two-way ANOVAS.

Sphagnum length increment and dry matter production over the summers of 2001 and 2002 were also analyzed with repeated-measures multivariate ANOVAS with year as the within-subject factor and summer treatment and winter treatment as the between-subject factors. Capitulum bulk density, subcapitulum bulk density and VPD were analyzed for main effects and interactions of the summer treatments and the winter treatments using two-

way ANOVAS. *Post hoc* multiple comparison tests (Bonferroni) were included in all analyses if winter treatment was a significant factor. Data were tested for homogeneity of variances with Levene's test of equality of error variances. The temperature data and the snow data did not meet those requirements in some periods, even after ln-transformation. Since analysis of variance is robust to considerable heterogeneity of variances as long as the sample sizes are nearly equal (Zar, 1999), we proceeded with the analyses without transformations. All analyses were performed with SPSS for Windows 10.1.

RESULTS

Winter conditions

The presence of OTCs in the winter snow addition plots and the winter snow addition plus spring warming plots increased the snow thickness two- to three-fold between October and April (Fig. 1). Especially from February to April, the period of highest ambient snow cover, the effect of the OTCs was very strong ($P < 0.001$). The snow addition treatments had slightly more weeks with snow cover in 2000-2001, which was related to the fewer weeks without snow during the period of unstable snow cover in early winter (data not shown). In 2001-2002, however, there was no clear effect of the treatments on the number of weeks with snow (data not shown), because the snow accumulation in November and December was much greater than in the previous winter (Fig. 1). In late-April and May 2001, the snow cover was significantly higher in the snow addition plus spring warming treatments ($P < 0.01$; Fig. 1), because the above-ambient snow levels and OTCs had already been removed from the winter snow addition without spring warming treatments (AS, WS). However, also in the snow addition plus spring warming plots the thin snow layer thawed within two weeks in 2001 and even within a week in 2002.

The increased snow thickness in winter resulted in strong increases in the average temperatures and average daily minimum and maximum temperatures of both air and soil (Fig. 2, see Table 2 for effect sizes and significance levels). In spring, the presence of the OTCs in the AS + and WS + treatments increased the air average and daily maximum temperatures in 2002 and soil average and daily maximum temperatures in both years (Fig. 2, Table 2). The start of the growing season, indicated by an average temperature above 5 °C, was enhanced by 4-6 days (Table 2).

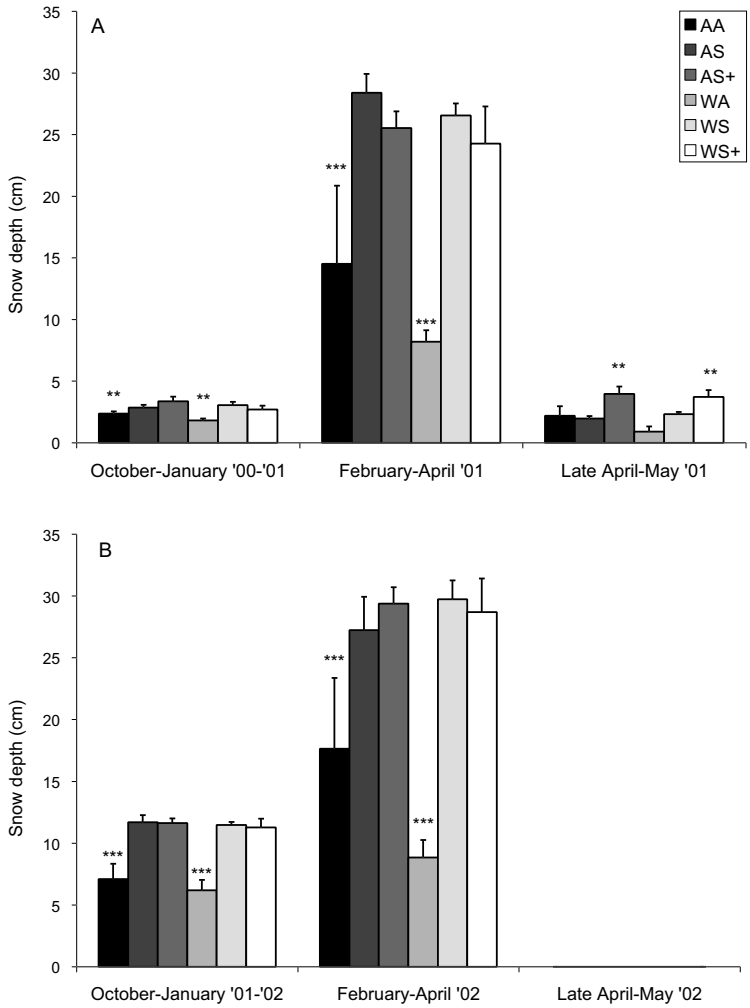

Fig. 1 Mean (+ SEM, n = 5) snow depths as a result of passive snow accumulation in OTCs (treatments AS, AS +, WS and WS +) in comparison with ambient snow height (treatments AA and WA), in the winters of 2000-2001 (A) and 2001-2002 (B). Bars with asterisks differ significantly from bars without asterisks within the same period (** $P < 0.01$; *** $P < 0.001$). For treatment codes, see Table 1.

Summer conditions

In summer, the OTCs significantly increased the average air temperature in June and July, but not in August and September (Fig. 2, see Table 2 for effect sizes and significance levels). The average soil temperatures were not significantly affected. Summer warming also increased the daily maximum air and soil temperatures throughout the summer. The temperature increase in the summer warming plots in June and July 2002 was accompanied by a higher relative air humidity. The average VPD was therefore not significantly affected

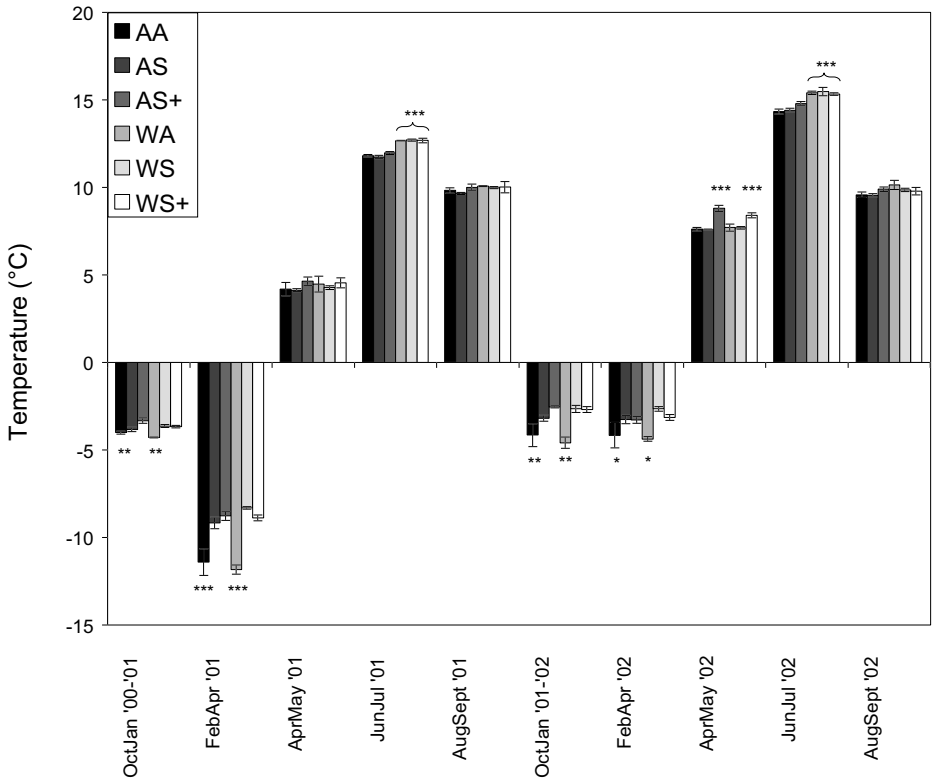

Fig. 2 Mean (± SEM, $n = 3$) air temperatures at 5 cm above the *Sphagnum* carpet in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming). Bars with asterisks differ significantly from bars without asterisks within the same period (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). For treatment codes, see Table 1.

by the different climate change scenarios (Table 3), although there was a trend for a slightly lower VPD in the warming treatments (summer treatments $P = 0.08$, winter treatments $P = 0.14$, interaction $P = 0.99$).

Sphagnum *length growth*

Summer warming significantly enhanced the average summer length increment of *S. fuscum* by 62 % in 2001 and by 42 % in 2002 ($P = 0.01$; Fig. 3, Table 4). There was no significant effect of the winter snow addition and the spring warming treatments on *Sphagnum* summer growth ($P = 0.88$). The responses showed similar patterns in both years, but the absolute growth values were 31 % higher in 2002 ($P < 0.001$), which had a much warmer summer (Fig. 2). The differences in length increment between the treatments were apparent throughout the growing season in both years (data not shown). The length growth

Table 2 Increases of temperature parameters by OTCs in winter (October-January, February-April), spring (late April-May) and summer (June-July, August-September) in 2001 and 2002 (n = 3)

	Winter			
	October-January		February-April	
	2000-2001	2001-2002	2001	2002
Air temperature				
Daily average T (°C)	0.5**	1.6**	2.8***	1.2*
Daily minimum T (°C)	0.8***	2.2**	4.4***	2.5*
Daily maximum T (°C)	0.3*	1.1*	1.2*	0.04*
No. of days average T > 5 °C	- 0.8	- 0.6	0	- 0.2
Soil temperature				
Daily average T (°C)	0.5*	0.9*	2.2***	0.9* (1)
Daily minimum T (°C)	0.6*	1.1*	2.8***	1.3* (1)
Daily maximum T (°C)	0.3	0.7*	1.5*	0.3
No. of days average T > 5 °C	- 1.3	- 0.1	0	0.3

Unless otherwise indicated, the difference between the average parameter value of the snow addition treatments (AS, AS +, WS, WS +) and the average of the winter ambient treatments (AA, WA) is given in winter. In spring, the difference is calculated between the average of the spring warming treatments (AS +, WS +) and the average of the spring ambient treatments (AA, AS, WA, WS), and in summer the difference between the average of the summer warming treatments (WA, WS, WS +) and the average of the summer ambient treatments (AA, AS, AS +). Asterisks indicate the highest P-value of the two *post hoc* comparisons for each parameter in winter and spring and the significance level of the summer effect in summer, according to the repeated measures procedure as described in the Materials and methods section. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. (1) Difference between the average of AS and WS and the average of AA and WA.

Table 3 Average vapor pressure deficit (kPa) in June and July 2002 in the plots of the summer and winter climate change scenarios (mean ± SEM, n = 5)

	Summer treatment	
Winter treatment	Ambient	Warming
Ambient	1.54 ± 0.09	1.41 ± 0.11
Snow addition	1.62 ± 0.07	1.51 ± 0.04
Snow addition plus spring warming	1.46 ± 0.03	1.36 ± 0.08

Table 2 Continued

	Spring		Summer			
	Late-April-May		June-July		August-September	
	2001	2002	2001	2002	2001	2002
Air temperature						
Daily average *T* (°C)	0.3	1.0***	0.9***	0.9***	0.2	0.3
Daily minimum *T* (°C)	0.1	- 0.1	- 0.1	- 0.3	- 0.4	- 0.3
Daily maximum *T* (°C)	0.7	2.3***	2.3***	2.6***	1.1**	1.1**
No. of days average *T* > 5 °C	5.8**	4.1**	0	0	0	0.2
Soil temperature						
Daily average *T* (°C)	0.7*	1.2*	0.9	0.6	0.4	0.5
Daily minimum *T* (°C)	0	0.3	0.3	0.1	0.1	- 0.2
Daily maximum *T* (°C)	1.6*	2.4*	1.6*	1.1*	0.8*	1.3*
No. of days average *T* > 5 °C	5.6*	4.6*	0.2	0	1.1	0.3

rate was highest in June and July, during which months 78 % (2001) and 69 % (2002) of the length increment took place (data not shown). This corresponds to the part of the summer with the highest average and daily minimum and maximum temperatures.

Sphagnum *carpet structure*

The capitulum bulk density and the bulk density just below the capitula showed similar responses to the climate change scenarios (Fig. 4). The summer warming treatments significantly reduced the capitulum bulk density ($P = 0.01$), but the winter treatments had no significant effect ($P = 0.46$), nor was there a significant interaction between the summer and winter treatments ($P = 0.39$). The bulk density of the *Sphagnum* tissues directly below the capitula also decreased due to summer warming ($P = 0.03$). There was no significant difference between the three winter climate change treatments ($P = 0.22$) and no interaction ($P = 0.54$).

Sphagnum *production*

Even though the effects of the summer warming treatments on length growth and bulk density were opposite (Figs 3 and 4), there was a trend ($P = 0.09$) for a positive effect on the dry mass production during both summers (Fig. 5, Table 4). In contrast to length increment and carpet structure, the dry matter production showed a significant and positive

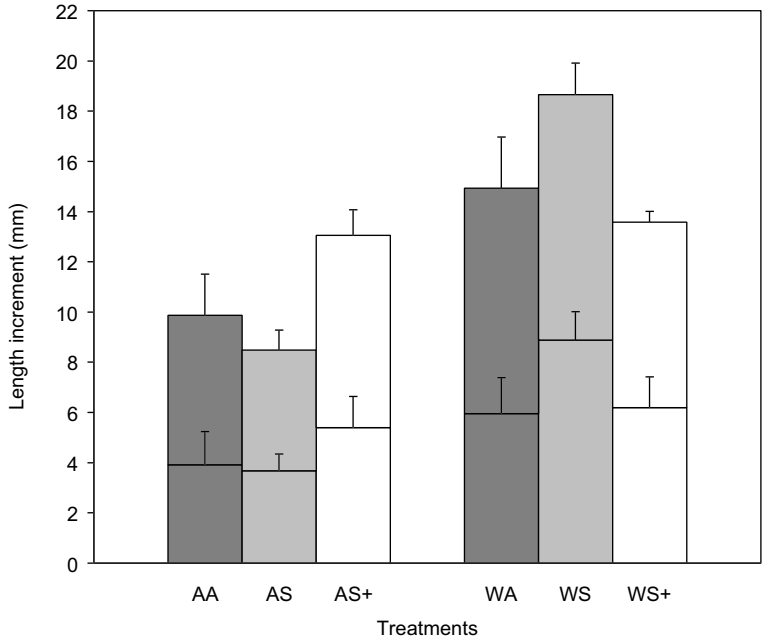

Fig. 3 Summer length increment of *Sphagnum fuscum* in 2001 (lower part of each bar) and 2002 (upper part of each bar) in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming). Mean + SEM for each treatment and each year (n = 5) are indicated. For treatment codes, see Table 1.

Table 4 Repeated measures ANOVA P-values for the effects of summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) on *Sphagnum fuscum* length increment and production during the summers of 2001 and 2002 (n = 5)

Source	Length increment	Production
Year	< 0.001	< 0.001
Year × summer	0.85	0.37
Year × winter	0.10	0.23
Year × summer × winter	0.32	0.63
Summer	0.01	0.09
Winter	0.88	0.04
Summer × winter	0.16	0.30

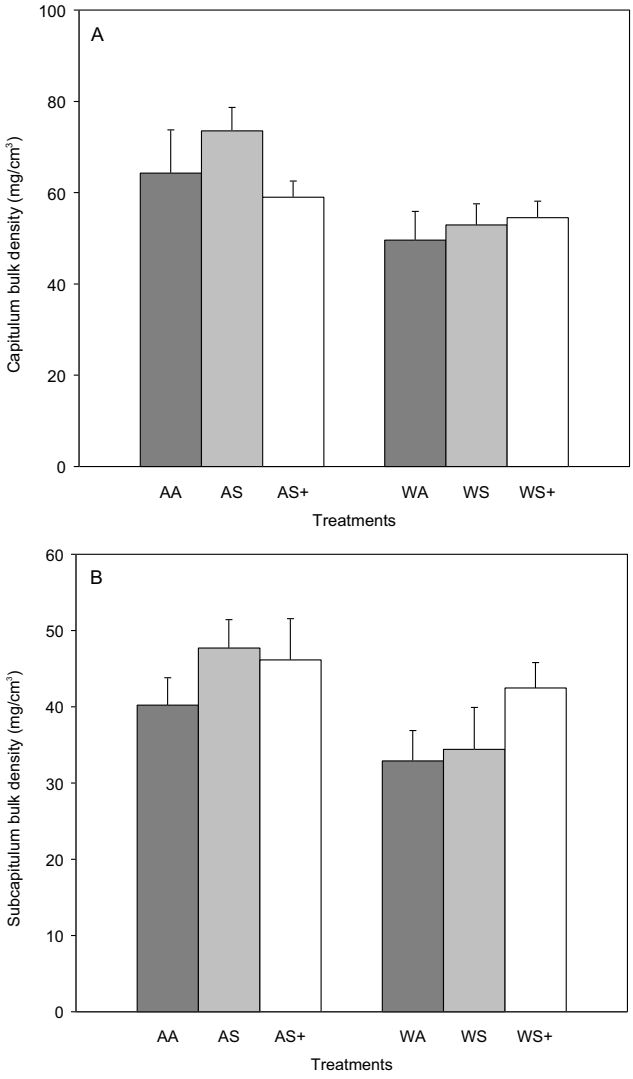

Fig. 4 Effects of summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) on *Sphagnum fuscum* (A) capitulum bulk density and (B) the bulk density directly under the capitula at the end of the growing season 2002 (mean + SEM, $n = 5$). For treatment codes, see Table 1.

response to the winter and spring treatments ($P = 0.04$). However, only the effect of winter snow addition in combination with early-spring warming on the total summer production was significant relative to winter ambient conditions (Fig. 5). There was no difference between the 2 years in the response to the climate change scenarios. However, in 2002 the differences between the treatments were smaller than in 2001. This was probably due

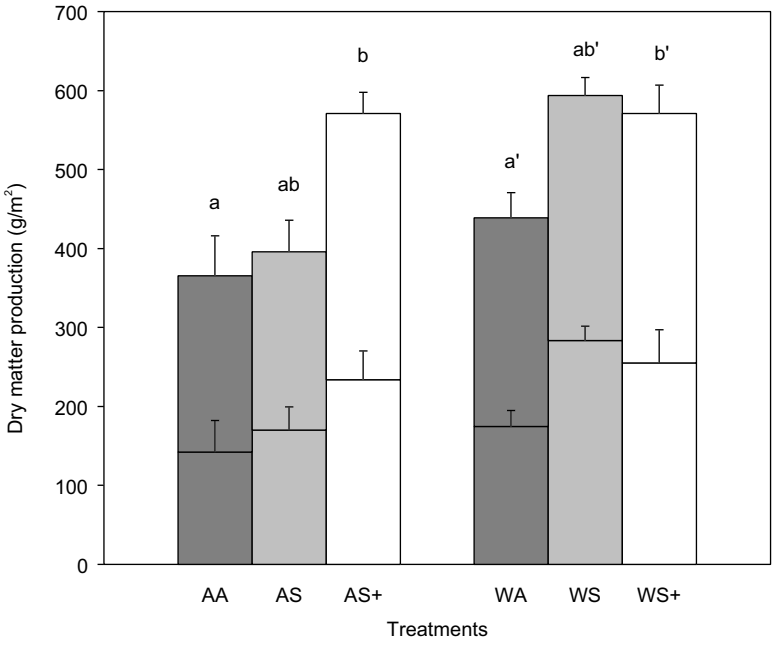

Fig. 5 Dry matter production of *Sphagnum fuscum* during the summers of 2001 (lower part of each bar) and 2002 (upper part of each bar) in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming). Mean + SEM for each treatment and each year (n = 5) are indicated. Different letters indicate significant differences (P < 0.05) in total production between the winter scenarios within the summer ambient and summer warming treatment, respectively. For treatment codes, see Table 1.

to the stronger response in production in the summer ambient treatments as a result of the higher ambient temperatures during the summer of 2002. These results indicate that the positive response to summer warming is limited with respect to the range over which the temperature increase takes place.

There was no significant interaction between the summer treatments and the winter treatments (P = 0.30; Table 4), which indicates that the effects of summer warming and winter/spring conditions were additive. Figure 6 shows that the six climate scenarios had different effects on the balance between investment in bulk density and length increment of *S. fuscum*. The summer warming treatments show on average a strong rightwards and slightly downwards shift in the graph, which indicates that the apparent effect of summer warming on the production was through its strong, positive effect on the length increment, despite the smaller decrease in bulk density. The two winter manipulations had on average a small, but positive effect on the summer length increment (+ 8.5 %, Fig. 3) compared with the winter ambient treatments, but they also had a positive and larger effect on the

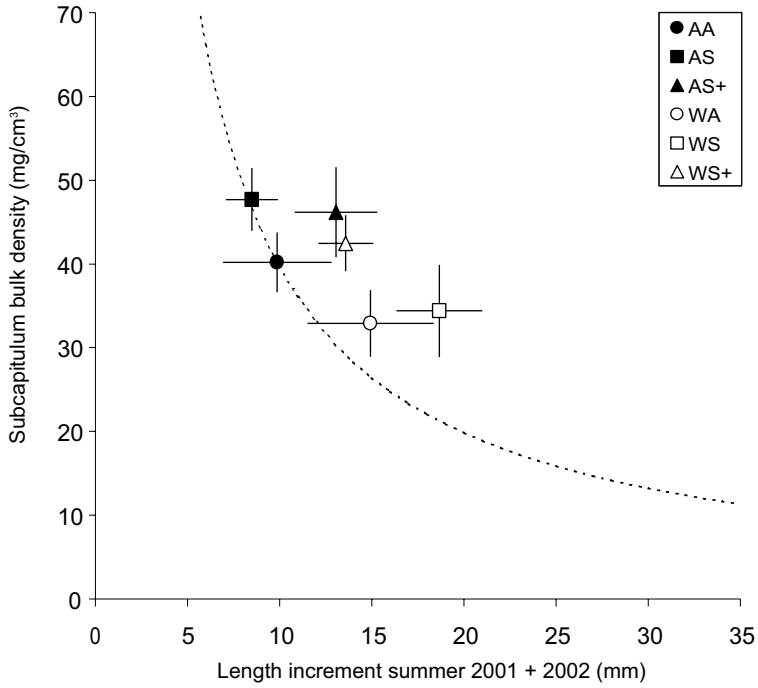

Fig. 6 Total *Sphagnum fuscum* length increment during the summers of 2001 and 2002 and its subcapitulum bulk density in relation to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) (mean ± SEM, $n = 5$). The dotted line is fitted to the theoretically possible combinations of length increment and bulk density that would give a production equal to the production in the AA treatment. All points above this line have a higher production. For treatment codes, see Table 1.

bulk density (+ 16.8 %, Fig. 4). This indicates that, even though both separate effects were not significant, the strong and positive effect of the winter manipulations on biomass production (+ 32.5 % on average, Fig. 5) were primarily due to an increase in bulk density of the *Sphagnum* carpet.

DISCUSSION

Environmental conditions

The global average temperatures are predicted to increase by 1.4-5.8 °C in this century, but there will be a substantial variation between regions and seasons (Houghton *et al*., 2001). The amount of precipitation at northern high latitudes is likely to increase as well (Houghton *et al*., 2001). In our experiment, we therefore created six different scenarios that combined changes in summer and winter climate, using transparent OTCs. The effects of the OTCs

on summer and winter temperature and snow cover were quite distinct. Model projections for climate change in arctic and sub-arctic areas indicate a particularly high increase in winter temperature, varying from 2.0 to as much as 14.0 °C, and a 5-20 % higher snowfall over Northern Europe (Maxwell, 1992; Houghton *et al*., 2001; McCarthy *et al*., 2001). In winter, our OTCs doubled the snow thickness (Fig. 1), which enhanced the average air and soil temperatures by 0.5-2.8 °C (Fig. 2, Table 2). Spring temperatures increased by 0.7-1.2 °C inside the OTCs. Winter snow manipulations in previous studies have mostly involved snow fences, which may result in snow depths of 1 up to 3 m relative to ambient snow levels of 0.3-0.5 m (Walsh *et al*., 1997; Jones *et al*., 1998). This is beyond realistic predictions of winter snowfall increases, while temperature recordings from these studies are lacking.

Summer temperatures at northern high latitudes are predicted to increase by 1.0-8.2 °C (Maxwell, 1992; Houghton *et al*., 2001; McCarthy *et al*., 2001). Summer precipitation in these areas is expected to show a smaller increase than winter precipitation, although predictions vary considerably between regions (Houghton *et al*., 2001). The effects on moisture availability will strongly depend on the balance between precipitation, snowmelt timing and factors affecting evapotranspiration, such as temperature and cloud cover. In summer, the effect of our OTCs on the average air temperature was smaller than in winter, with a maximum increase of 0.9 °C in June-July (Fig. 2, Table 2). The average soil temperature was not affected. VPD was also not affected (Table 3), indicating that increased summer temperatures do not necessarily affect moisture conditions negatively. The temperature enhancement we found seems to be at the lower end of the range of 1.2-1.8 °C summer warming reported for similar open-top simulations (Marion *et al*., 1997). This may be a consequence of the larger size of the OTCs we used, in order to cope with the large area covered by some of the clonal vascular plants in sub-arctic peatlands and to minimize edge effects on the micro-climate. Also, compared with the projections for future climate change, the increases in temperature resulting from our summer and winter manipulations were relatively small, but probably very realistic for the upcoming decades. However, even under these conservative scenarios, we found strong responses in growth, structure and production of *S. fuscum*.

Responses to changes in summer conditions

The summer warming treatments had a strong, positive effect on the length increment of *S. fuscum* and there was a trend for an increase in biomass production (Figs 3 and 5, Table 4). This resulted in a distinct reduction in both capitulum bulk density and subcapitulum bulk density (Fig. 4). These findings are contrary to our expectations and the results of previous experiments. Weltzin *et al*. (2001) found that the annual production of *Sphagnum* was unaffected in a mesocosm experiment using infrared lamps to increase the soil

temperatures. The production strongly declined in a year when the treatment resulted in desiccation of the mosses. In a field experiment using plastic greenhouses, no effects on total *Sphagnum* biomass were found either, but there was a strong increase in VPD (Hobbie & Chapin, 1998; Hobbie *et al*., 1999). *Sphagnum* photosynthesis is highly sensitive to decreases in hydration (Titus *et al*., 1983; Silvola & Aaltonen, 1984). In our experiment, neither VPD nor water table depth (after three whole years of treatment, S Toet, personal communication) were affected. The results we report here therefore indicate that a realistic increase in summer temperatures will not necessarily lead to moisture conditions that are sub-optimal for *Sphagnum* length growth and production. In such cases, the relatively high optimum temperature for photosynthesis of *Sphagnum* mosses (Skre & Oechel, 1981; Harley *et al*., 1989) explains the positive response in length growth and the trend for a positive response in production to summer warming.

The enhanced summer temperatures also appeared to have strong effects on the structure of the *Sphagnum* carpet (Fig. 4). The increased length growth was not accompanied by an equally strong increase in biomass production, which resulted in a marked reduction of the capitulum bulk density and the subcapitulum bulk density. Sonesson *et al.* (2002) also found a strong increase in length growth in *S. fuscum*, while Hobbie *et al*. (1999) reported a reduction in capitulum mass in response to summer warming. Structural changes in the moss layer are very likely to affect the long-term hydrological conditions in the *Sphagnum* carpet. *Sphagnum* plants are poikilohydric and the supply of water to the active apical parts of the plants, where the growth and photosynthesis are located, is through capillary rise of water along the stem and between the stem and the branches (Clymo & Hayward, 1982). Hummock-forming *Sphagnum* species, such as *S. fuscum*, are well known for their highly efficient external capillary system and their ability to retain moisture at high levels above the water table, due to their dense structure (Clymo & Hayward, 1982; Wagner & Titus, 1984; Lindholm, 1990). A decrease in bulk density will eventually reduce the water supply to the surface tissues. It therefore seems likely that the changes in structure will hamper the future productivity of *Sphagnum*.

Responses to changes in winter conditions

Increased winter snow cover had a positive effect on the production of *S. fuscum* (Fig. 5, Table 4), which was more related to an increase in bulk density than to an increase in length increment (Fig. 6). The high bulk density associated with the increased production in the snow addition plots may partly have been the result of compression of the shoots by the heavier snow loads in winter. Lindholm & Vasander (1990) reported that the effects of the snow in southern Finland, estimated to be 100-120 kg m^{-2} at the end of March, were clearly visible in spring for long upright shoots. For dense *S. fuscum* carpets, however, the

weight per shoot is relatively low and the compression by snow only slight (Pakarinen and Tolonen, 1977 in Lindholm & Vasander, 1990). This is confirmed by winter measurements of *S. fuscum* length increment by Sonesson *et al*. (2002), who found a decrease in capitulum height of approximately 0.25 mm. The snow loads in our snow addition plots reached maximum values in late winter up to 80-100 kg m^{-2} (measured in April 2001). The average length increment in the snow addition plots was 7.4 mm in the last summer before the bulk density was determined. It is therefore unlikely that compression by snow alone can explain the measured increase in bulk density.

Biomass production is the result of photosynthetic activity, which is primarily located in the capitula, especially in the dense carpets of *S. fuscum*. *Sphagnum* photosynthesis at the beginning of the growing season is characterized by low optimum temperatures and low maximum rates, due to high respiration for the restoration of photosynthetic tissues in the capitula, after substantial damage during the winter (Skre & Oechel, 1981; Daggit in Clymo & Hayward, 1982). The accumulation of up to 30 cm of snow in our OTCs during the winter months increased both the average and minimum temperatures substantially, which may have prevented damage to the capitula and resulted in a positive effect on the production of *S. fuscum*. Malmer & Wallén (1996) compared the formation of litter in the acrotelm of *S. fuscum* hummocks in the Abisko area, and they also found that increasing snow depths along a natural gradient from east to west were correlated with a doubling of the productivity. However, as we have not measured the moisture content of the mosses, we cannot exclude a role of increased hydration of the capitula either.

The addition of spring warming to the snow addition treatments resulted in slightly further enhancement of biomass production, although the difference compared to snow addition alone was not significant (Fig. 5). Owing to practical constraints, we started the growth measurements in late-May/early-June and continued until the end of September. We may thus have excluded the earliest growth in the spring warming treatments. *S. fuscum* length increments under ambient winter and spring conditions have been found to be approximately -0.25 mm from September until the beginning of June (Sonesson *et al*., 2002). The growing season is reported to begin when the temperature rises above 5 °C (Backéus, 1988), at which temperature the net photosynthesis is only 40-50 % of its maximum (Harley *et al*., 1989). Spring warming increased the average number of days with an average soil temperature above 5 °C before the start of our measurements from 3.6 to 9.2 in 2001 and from 11.4 to 16.0 in 2002, compared with the snow addition and winter ambient treatments. Especially in the warm growing season of 2002, we may therefore have underestimated the total length growth and production in the spring warming treatments.

Long-term implications of climate change

Changes in summer and winter climate strongly affected production, length growth and carpet structure of *S. fuscum* within the first 3 years of the manipulations. Such changes may affect the competition between moss species (Rydin, 1997), but experimental results obtained so far are inconclusive. Sonesson *et al*. (2002) found no effect of 2 years of summer warming on the competition between *S. fuscum* and *Dicranum elongatum*. On the other hand, Weltzin *et al.* (2001) reported that a reduction in the cover of *Sphagnum* Sect. *Acutifolia* under infrared lamps was accompanied by an increase in the cover of *Polytrichum strictum* and *S. magellanicum*. In our study site, the moss layer consists of a rather homogeneous *S. fuscum* cover. Changes in the hydrological regime due to the reduced density of the *Sphagnum* carpet will decrease the probability of a successful invasion by other, more demanding *Sphagnum* species. Future changes in the abundance of the *Sphagnum* mosses due to competition therefore do not seem very likely. However, increased length growth rates may also affect the relation between *Sphagnum* and vascular plants. Most of the higher plants growing in bogs have annual shoot growth rates similar to the *Sphagnum* mosses in order not to become buried within the moss layer (Rydin, 1997). The roots and shoots of the vascular plants also form the matrix that supports the height increment of hummock-forming *Sphagnum* species (Malmer *et al*., 1994). Changes in climate may disturb this balance when the growth rates of *Sphagnum* and of vascular plants show different responses. Shoot growth rates of most vascular plant species seem to be stimulated by experimental warming, but the degree of their response may vary. The annual shoot length increments of *Vaccinium vitis-idaea* and *Betula nana*, for example, were enhanced by approximately 30 % and more than 100 %, respectively, after 2 years of summer warming (Hobbie *et al*., 1999). This indicates that the 42-62 % increase in *S. fuscum* length increment as a response to our summer warming treatments, may indeed form a threat to slow-growing, small shrubs. On the other hand, the increased height of tall shrubs, such as *Betula nana*, in response to summer warming or a thicker snow cover (Sonesson, 1969) may suppress *Sphagnum* growth and production through increased shading.

The changes in climate predicted for northern high latitudes will affect the carbon budgets of areas with important carbon storage functions. Total ecosystem respiration in wetland mesocosms was found to increase by 15-35 % in response to increased soil temperatures (Updegraff *et al*., 2001). Jones *et al*. (1998) found similar results for ecosystem respiration in moist tundra in Alaska. This is in the same range as the average apparent increase in production of *S. fuscum* in our summer warming treatments (21 %; Fig. 5). Winter snow addition enhanced ecosystem respiration even more in moist tundra, especially in combination with summer warming, but not in dry tundra (Jones *et al*., 1998). The dry matter production of *S. fuscum* in our summer warming and winter snow addition

treatments increased by 60 % compared with the summer and winter ambient plots. Because there was no effect on the structure of the *Sphagnum* carpet, the enhanced production of *S. fuscum* in response to winter snow addition has the potential to contribute to changes in the long-term carbon balance of northern peatlands. On the other hand, future responses of production to summer warming seem to be strongly dependent on longer-term interactions with other plants as well as to environmental conditions related to moisture availability.

In this study, we manipulated summer temperature and winter snow cover in combination with spring temperatures, which resulted in six different scenarios of future climatic conditions. The distinct responses in length growth, carpet structure and biomass production of *S. fuscum* indicate that it is necessary to include several scenarios of both summer and winter climate in manipulative climate change studies, and that we need detailed projections of future climate at a regional scale in order to assess their impacts on natural ecosystems.

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CHAPTER 3

SPHAGNUM MODIFIES CLIMATE CHANGE IMPACTS ON SUB-ARCTIC VASCULAR BOG PLANTS

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Submitted

SUMMARY

1. Vascular plant growth forms in northern peatlands differ in their strategies to cope with the harsh climate, low nutrient availability and progressively increasing height of the *Sphagnum* carpet in which they grow. Climate change may therefore differentially affect them, both directly and through changes in the length growth of *Sphagnum* mosses. However, the role of mosses as modifiers of climate-change effects on vascular plants has been largely overlooked so far. We investigated the direct and *Sphagnum*-mediated effects of experimental changes in summer, winter and spring climate on four species of contrasting growth forms (evergreen and deciduous shrubs, graminoid, forb) in a sub-arctic bog, by studying their biomass and nitrogen (N) losses through leaf litter, and the length growth of the two shrubs.

2. Direct and indirect effects of summer warming differed among the growth forms. Enhanced *Sphagnum* overgrowth of leaves due to summer warming initially stimulated

leaf litter losses of the evergreen shrub *Empetrum nigrum*. However, changes in its shoot morphology, related to an apparent, small increase in its length growth, prevented further effects. A stronger increase in stem growth of the deciduous shrub *Betula nana* in response to summer warming directly reduced its leaf litter mass, N concentration and N losses. The changed allocation prevented indirect, *Sphagnum*-mediated effects on its leaf and N dynamics through overgrowth of buds. In contrast, leaf litter mass, N concentrations or N losses of the forb *Rubus chamaemorus* and the graminoid *Calamagrostis lapponica* were not affected by summer warming or enhanced *Sphagnum* growth.

3. Increases in winter snow cover, with or without spring warming, did not affect shrub growth, nor the total shoot leaf litter mass or N dynamics of any of the growth forms.

4. Altogether, summer warming is likely to enhance *Sphagnum* overgrowth of small shrubs with a limited growth response, such as *Empetrum*. Moreover, increased vertical growth may allow *Sphagnum* to keep pace with inclined growing, responsive shrubs like *Betula*. This may prevent net positive effects of summer warming on the canopy height, and negate longer-term benefits of enhanced snow cover for these taller shrubs. However, leaf litter production and related nutrient dynamics are more likely affected by direct warming effects on shoot morphology and allocation than by *Sphagnum* growth. The different responses of the growth forms to summer warming suggest that both direct and *Sphagnum*-mediated climate effects have the potential to change the vascular plant community structure and nutrient dynamics in peatlands.

INTRODUCTION

Plant growth and survival in high-latitude ecosystems are constrained by adverse environmental conditions, such as low temperatures and irradiance throughout a large part of the year, a short growing season, and low nutrient availability (Bliss 1956, Sonesson & Callaghan 1991, Arft et al. 1999). In northern peatlands, vascular plant performance is further controlled by the presence of *Sphagnum*, which often dominates the bottom-layer and the peat deposits in which the plants grow (Clymo & Hayward 1982). *Sphagnum* mosses strongly reduce the nutrient availability to vascular plants by efficiently accumulating nutrients from atmospheric deposition and reducing decay and mineralisation rates (Lee & Woodin 1988, Malmer et al. 1994, Van Breemen 1995, Li & Vitt 1997). At the same time, however, they force vascular plants to keep pace with their progressively increasing height, in order not to become buried (Backéus 1985, Malmer et al. 1994, Rydin 1997). The abiotic and biotic environment thus poses extreme demands on vascular plant growth and nutrient use efficiency in northern peatlands. Arctic and sub-arctic areas are expected to experience above global-average increases in year-round temperatures and winter precipitation during

this century (Maxwell 1992, Houghton et al. 2001, McCarthy et al. 2001). This may directly alleviate climatic and possibly nutritional constraints on vascular plants (Chapin et al. 1995, Rustad et al. 2001). However, strongly enhanced *Sphagnum* growth as a result of climate change (Sonesson et al. 2002, Dorrepaal et al. 2003) may modify the net effects on community structure and nutrient dynamics in northern peatlands.

The growth strategies that enable vascular plants to cope with the contrasting abiotic and biotic demands in northern peatlands might be indicative of their sensitivity to the direct and *Sphagnum*-mediated effects of climate change as well. Deciduous and evergreen shrubs, which make up a major part of many vascular plant communities of peatlands, have long-lived, woody stems with low nutrient concentrations, which limit their nutrient requirements (Berendse et al. 1987, Berendse & Jonasson 1992). Evergreen shrubs reduce their litter production and nutrient losses even further by having an extended leaf longevity and very low litter nutrient concentrations (Aerts 1995, Eckstein & Karlsson 1997). However, aboveground woody shoots carry a great risk of winter frost damage to apical buds and branches, or over-wintering leaves, if the protection of a snow cover is limiting (Sonesson 1969, Weih & Karlsson 2002). Moreover, shrubs must compensate the yearly decrease in branch height (relative to the vertically up-growing *Sphagnum* carpet) by new growth at the top of their usually inclined branches (Backéus 1985, Malmer et al. 1994). Clonal graminoids and forbs, on the other hand, avoid frost damage or *Sphagnum* overgrowth of their shoots, by abandoning their aboveground tissues (including the non-resorbed nutrients) at the end of the growing season. During the coldest part of the year, they thus keep their growing points just below the moss surface, and efficient elongation of their below-ground rhizomes enables their shoots to keep pace with the *Sphagnum* surface in summer (Backéus 1985, Malmer et al. 1994, Svensson 1995). However, as a consequence, graminoids and forbs lose a large proportion of their nutrients annually through the formation of litter (Berendse et al. 1987, Berendse & Jonasson 1992, Eckstein & Karlsson 1997).

The climatic and nutritional conditions, together with the growth rate of *Sphagnum*, control the relative importance of the benefits and disadvantages of each of the growth strategies. However, in contrast to the direct effects of higher summer temperatures on plant performance at high latitudes, effects of changes in climate outside the growing season, and indirect, *Sphagnum*-mediated effects of summer warming in northern peatlands have received little attention so far. Summer warming may directly increase the growth of deciduous and evergreen shrubs (Parsons et al. 1994, Shevtsova et al. 1997, Hobbie et al. 1999, Bret-Harte et al. 2002), but their response tends to be smaller than observed for *Sphagnum* (Sonesson et al. 2002, Dorrepaal et al. 2003). Summer warming may therefore increase the risk of shrubs becoming overgrown. The performance of small evergreen shrubs may be further

suppressed by increased leaf turnover and nutrient losses through enhanced senescence of basal leaves overgrown by *Sphagnum* (Backéus 1985). Furthermore, enhanced overgrowth of the basal leaf buds of deciduous shrubs may prevent net positive effects of increased temperatures on their leaf and biomass production (Chapin & Shaver 1985, Hobbie et al. 1999, Suzuki & Kudo 2000), and thus potentially on carbon sequestration in peatlands. Changes in climatic conditions outside the growing season do not seem to affect *Sphagnum* length growth (Dorrepaal et al. 2003). However, positive relations between *Betula nana* shrub height (Sonesson 1969), or *Betula pubescens* seedling leaf biomass (Weih & Karlsson 2002), and winter snow thickness indicate that the aboveground over-wintering shoots of tall shrubs in particular may benefit from the increased protection of a thicker snow layer. Higher spring temperatures may accelerate vascular leaf development and early season growth, although the responsiveness of species varies (Backéus 1985, Chapin & Shaver 1996, Shevtsova et al. 1997, Arft et al. 1999, Suzuki & Kudo 2000). It remains uncertain, however, whether these early-season, phenological effects alone will increase the total growing-season shoot elongation and leaf production, without additional warming during the rest of the summer (Backéus 1985, Shevtsova et al. 1997, Kudo et al. 1999).

In this study we investigated the responses of different vascular plant growth forms to experimentally imposed changes in summer, winter and spring climate (temperatures, snow cover thickness) in a sub-arctic bog in north Sweden. We explicitly attempted to differentiate between direct and *Sphagnum*-mediated effects of summer warming, and particularly examined potential, negative, *Sphagnum*-mediated effects on shrubs. In order to do this, we related shoot biomass and nitrogen (N) dynamics through leaf litter of four species of contrasting growth strategies, viz. *Empetrum nigrum* (short evergreen shrub), *Betula nana* (taller deciduous shrub), *Rubus chamaemorus* (forb), and *Calamagrostis lapponica* (graminoid), and length growth of the two shrubs, to *Sphagnum* length growth. We tested the following hypotheses. (I) Summer warming and higher spring temperatures will stimulate the length growth of shrubs, but relatively less than *Sphagnum* length growth. (II) Summer warming and higher spring temperatures will enhance leaf production and thus directly increase leaf litter and N losses of deciduous species (deciduous shrub, forb and graminoid), but not of evergreen shrubs. (III) Increased *Sphagnum* growth will (a) reduce basal bud development and thus leaf litter and N losses of deciduous shrubs, (b) stimulate basal leaf senescence and thus leaf litter and N losses of evergreen shrubs, by overgrowth of the basal parts of shrubs, and (c) not affect forbs and graminoids. (IV) Increased winter snow accumulation will enhance growth and leaf (litter) production of taller shrubs more strongly than that of shorter shrubs, forbs and graminoids.

METHODS

Study site and experimental design

The climate manipulation experiment was established on a slightly sloping bog on the southern shore of Lake Torneträsk, Abisko, north Sweden (68°21'N, 18°49'E). The vegetation is dominated by a continuous and homogeneous carpet of *Sphagnum fuscum* (Schimp.) H. Klinggr. Other bryophytes and lichens are sparse. The vascular plant community is low and open (maximum shrub height 15 cm, average cover 20 %), and consists mainly of *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, *Rubus chamaemorus* L., *Andromeda polifolia* L., *Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh., *Betula nana* L., *V. uliginosum* L., and *Calamagrostis lapponica* (Wahlenb.) Hartm. The water table depth decreases up-slope from approx. -20 cm to -40 cm (July 2001), while permafrost depth is approx. -45 cm.

Since June 2000, 30 plots have been subjected to experimental manipulations of summer, winter and spring climate, together six fully factorial combinations of two summer treatments (ambient, warming) and three treatments during winter and spring. For brevity, the latter will be referred to as winter treatments (ambient, snow addition, snow addition plus spring warming) (n = 5, see Table 1). Full details of the experimental procedures and their effects on summer and winter microclimate are presented in Dorrepaal et al. (2003). In summary, large, transparent, hexagonal ITEX open-top chambers (OTCs; 50 cm high, 2.2-2.5 m bottom diameter; cf. Marion et al. 1997) were used to manipulate the climate throughout the year. They increased the average air temperatures (+5 cm) in June-July by 0.9 °C. Air temperatures in August-September, average soil temperatures (-5 cm) throughout the summer, and vapour pressure deficit were not significantly affected by the OTCs. During winter (October through April), the OTCs passively accumulated snow, thereby doubling the ambient snow cover thickness and increasing the average air and soil temperatures by 0.5-2.8 and 0.5-2.2 °C, respectively. In spring (May), before the start of the actual growing season, OTCs increased the average air and soil temperatures in the AS + and WS + treatments by 0.3-1.0 and 0.7-1.2 °C, respectively, but did not affect snow-melt timing.

Table 1 Experimental design and treatment codes used for the climate manipulations

	Summer treatment	
Winter treatment	Ambient	Warming
Ambient	AA	WA
Snow addition	AS	WS
Snow addition plus spring warming	AS +	WS +

Length growth, leaf litter production and litter N concentration

To compare the effects of changes in summer and winter climate on shrub growth and on vascular plant leaf litter production and N losses, we selected one species of each of four growth forms, viz. *Empetrum nigrum* (short evergreen shrub), *Betula nana* (taller deciduous shrub), *Rubus chamaemorus* (forb) and *Calamagrostis lapponica* (graminoid). At the experimental site, these four species comprise about 85 % of the aboveground vascular plant biomass (S. Bokhorst & J.H.C. Cornelissen, unpublished results). The species are further indicated by their genus names for brevity. Because these species are long-lived perennials, whose ramets are connected below the moss layer through overgrown stems (shrubs) or rhizomes (forbs and graminoids), we defined a shoot as a stem or tiller that emerged above the moss layer (Chapin & Shaver 1985). In the second and third year of the experiment, in mid-July 2001 and 2002, we randomly selected and marked ten *Empetrum* shoots, five *Betula* shoots (2001 only) and five *Calamagrostis* shoots in the central area of each plot. *Empetrum* has a lower branching rate in *Sphagnum* carpets than at drier, more exposed sites (Bell & Tallis 1973, Backéus 1985). We thus confined ourselves to unbranched shoots in order to reduce heterogeneity. *Betula* normally also grows along one main axis (long shoots) and rather infrequently shows conversion of short side-branches (short shoots) into new long shoots (Bret-Harte et al. 2002). For this species we therefore included the main axis with short shoots, and all long shoots that had been converted from short shoots since the start of the experimental treatments. The selected shoots of *Calamagrostis* were all solitary ramets of 1-2 years old, as indicated by the small number of attached, overwintering dead leaves (Chapin & Shaver 1985). For *Rubus*, we included all shoots within a fixed area of 55 x 55 cm in the centre of each plot.

Because of the inherent differences in growth and leaf senescence among the growth forms, we had to apply different methods for each species. To measure the annual length increment and leaf litter production of *Empetrum*, we used the clearly spatially separated distribution of green (live) and brown (dead) leaves along the shoots. This pattern is caused by the progressive overgrowth and senescence of basal leaves, which remain attached to the stem for more than a year. We marked each shoot with a piece of thin, plastified iron wire, just above the uppermost brown leaves, and measured the length of the remaining green part of the branch. In mid-July of the following year, we cut off each shoot at the marking point, measured the total length and the length of the part covered with brown leaves, and harvested all brown leaves of each shoot. To avoid underestimating the litter production, owing to losses of senesced leaves during the year, we discarded the few shoots that had lost leaves just below or above the marking. For *Betula*, we used the same five shoots in each plot in both years and measured the length of the current-year growth of the main axis. This part was identified using colour differences and scars of the terminal bud. To estimate

the leaf litter production per shoot, we counted the number of leaves on each shoot cohort, i.e. main axis parts formed in 2002, 2001, 2000 or earlier, including their short shoots, and cohort parts of short shoots converted to long shoots in 2002, 2001 or 2000. We randomly collected 40 dead leaves per plot directly after leaf senescence, in September 2001 and 2002. Leaf litter production per shoot was calculated by multiplying the number of leaves per shoot by the average mass per dead leaf. For *Rubus*, we counted the number of leaves of each shoot within the fixed area in July, and randomly collected 10 senesced leaves per plot in September 2001 and 2002. Leaf litter production per shoot was calculated as indicated for *Betula*. The five marked *Calamagrostis* shoots per plot were harvested after senescence in September 2001 and 2002 as well. All leaf litter material was oven dried (70°C, 48 h), weighed and ground. Total N concentration was determined by dry combustion on a Carlo Erba NA1500 CNS-analyser for the second leaf litter collections only. The N losses through leaf senescence per shoot were calculated by multiplying the N concentration by the leaf litter production per shoot in the corresponding year. All measurements of individual shoots within each plot were averaged for each species before the statistical analyses.

Statistical analyses

The effects of the summer and winter climate manipulations on *Empetrum* annual stem length increment and *Betula* current-year stem length in the second and third year of the experiment were analysed using repeated-measures multivariate ANOVAS (Pillai's trace). Year was the within-subject factor and summer treatment and winter treatment the between-subject factors. The overall effects of the climate manipulations on leaf litter production per shoot in the two subsequent years were analysed for each of the four species using repeated-measures multivariate ANOVAS as well. These were followed by two-way ANOVAS for separate years if significant interactions between year and summer treatment, winter treatment or summer × winter treatment were found. The overall relation between vascular plant leaf litter production and *Sphagnum* length growth was analysed for separate years, by calculating Pearson's correlation coefficients (Spearman's rho in case of non-homogeneous variances), and using the *Sphagnum* data from Dorrepaal et al. (2003). The total range of *Sphagnum* growth in all plots was partly the result of the summer warming treatments. We therefore assessed the relative contribution of direct climate effects and indirect effects via *Sphagnum* growth on vascular plant leaf litter production, in those cases where both the overall summer climate treatment and the overall correlation with *Sphagnum* growth were significant. In order to do this, we performed an analysis of covariance, with summer and winter treatments as fixed factors and *Sphagnum* growth as a covariate, and compared the F-values of the summer factor and *Sphagnum* growth. Leaf litter N concentrations and total N losses through leaf litter formation per shoot were analysed for main effects and

interactions of the summer and winter treatments using two-way ANOVAS. All data were tested for homogeneity of variances with Levene's test. For *Betula* length growth, *Betula* older shoot leaf litter production, and *Rubus* total N loss per shoot, ln-transformation improved the homogeneity of variances considerably, but this had no effect on *Empetrum* length increment in 2002-2003. Since analysis of variance is robust to considerable heterogeneity of variances as long as the sample sizes are nearly equal (Zar 1999), we included the untransformed data for *Empetrum*. All analyses were performed with SPSS for Windows 10.1.

RESULTS

Length growth

Summer warming strongly increased the current-year stem length of *Betula* (42% in 2001, 51% in 2002), but the apparent positive effect ($P < 0.1$) on *Empetrum* annual stem length increment was less pronounced (19% in 2001-2002, 12% in 2002-2003) (Fig. 1, Table 2). Although winter snow addition plus spring warming seemed to enhance the length growth of the shrubs too (Fig. 1), this effect was not significant. *Empetrum* length increment was higher in 2001-2002 than in 2002-2003, but the overall responses of each of the species to the treatments were similar in both years. The relative response of *Betula* to summer warming was almost equal to that of *Sphagnum* (50% increase; Dorrepaal et al. 2003). For *Empetrum*, however, the ratio of shrub length growth to *Sphagnum* length growth was lower in the summer warming treatments than in the summer ambient treatments (Fig. 2).

Leaf litter production

The direct and *Sphagnum*-mediated effects of the climate manipulations on litter production differed among the growth forms. Overall, *Empetrum* lost 22% more leaf litter mass in the summer warming treatments than in the ambient treatments in 2001-2002, but this effect was not maintained in the next year (Fig. 3, Table 2). Increased winter snow cover and spring warming had no effect on *Empetrum* leaf litter losses (Table 2). The length of the harvested *Empetrum* stem parts covered with brown leaves was positively related to *Sphagnum* growth in both years (2001-2002: Pearson $r = 0.38$, $P < 0.05$; 2002-2003: $r = 0.63$, $P < 0.001$), but total leaf litter mass was only significantly, positively related to *Sphagnum* growth in 2001-2002 (Table 3). Analysis of covariance showed that the overall positive effect of the summer warming treatments on *Empetrum* leaf litter production in 2001-2002 was primarily via the effects on *Sphagnum* growth (summer treatments $F = 0.78$, $P > 0.1$; *Sphagnum* growth $F = 5.49$, $P < 0.05$).

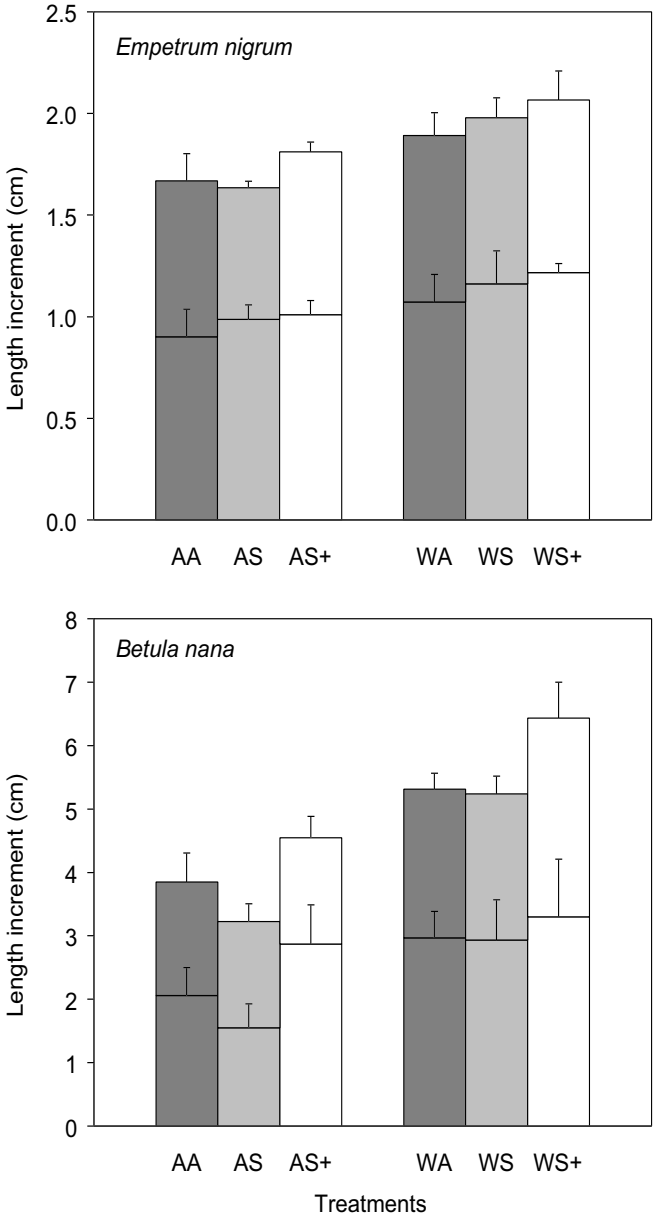

Fig. 1 Annual apical stem length increment of *Empetrum nigrum* (lower part of each bar: July 2001 - July 2002, upper part of each bar: July 2002 - July 2003), and current-year apical stem length of *Betula nana* (lower part of each bar: July 2001, upper part of each bar: July 2002) in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) (mean + SEM for each treatment and each period, n = 5). For treatment codes, see Table 1.

Table 2 Repeated-measures ANOVA and two-way ANOVA F-statistics (n = 5) for the effects of summer (ambient, warming; SUM) and winter treatments (ambient, snow addition, snow addition plus spring warming; WIN) on *Empetrum nigrum* annual stem length increment and *Betula nana* current-year stem length; and on leaf litter production per shoot of *Empetrum nigrum*, *Betula nana* (total shoot and current-year (C), previous-year (P), and older (O) parts separately), *Rubus chamaemorus* and *Calamagrostis lapponica* (Y = year)

	Source (df)						
	Y	Y × SUM	Y × WIN	Y × SUM × WIN	SUM	WIN	SUM × WIN
Variable and species	(1)	(1)	(2)	(2)	(1)	(2)	(2)
Apical growth							
Empetrum	43.11 ***	1.27	1.06	0.30	3.12 $^{+}$	0.40	0.06
Betula	1.26	0.14	0.24	1.28	7.77 **	0.85	0.14
Leaf litter mass							
Empetrum 2 years	12.47 **	5.59 *	1.82	1.22	1.96	0.33	0.12
Empetrum 2001-2002	-	-	-	-	4.38 *	0.94	0.30
Empetrum 2002-2003	-	-	-	-	0.18	0.68	1.14
Betula total shoot	24.41 ***	0.71	2.07	0.29	5.04 *	0.71	0.19
Betula C-shoot	1.86	0.14	0.85	0.45	0.19	5.34 *	0.16
Betula P-shoot 2 years	59.84 ***	4.38 *	0.71	1.64	1.50	2.28	0.88
Betula P-shoot 2001	-	-	-	-	5.55 *	1.19	0.03
Betula P-shoot 2002	-	-	-	-	0.00	2.33	1.79
Betula O-shoot	2.50	0.32	0.08	0.37	8.74 **	0.14	0.01
Rubus	0.02	0.31	0.18	1.63	0.86	0.89	1.44
Calamagrostis	0.64	0.28	1.01	1.22	0.00	1.46	0.54

Analyses include data for both 2001 and 2002 (*Empetrum* 2001-2002 and 2002-2003), unless otherwise indicated. Error df = 24. $^{+}$ P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001.

Betula leaf litter production was clearly reduced by the summer warming treatments in both years (-20% in 2001, -22% in 2002), but was not affected by the winter and spring treatments (Fig. 3, Table 2). This was primarily the result of a (non-significant) reduction in the total number of leaves per shoot (data not shown). On a total shoot basis, leaf litter production was negatively related to *Sphagnum* growth, although the correlation coefficients were not significant (Table 3). Analyses of the separate shoot cohorts showed that the climate manipulations and increased *Sphagnum* growth had different effects on the basal and apical parts of the shoots (Fig. 4, Table 2). The production of leaf litter by the current-

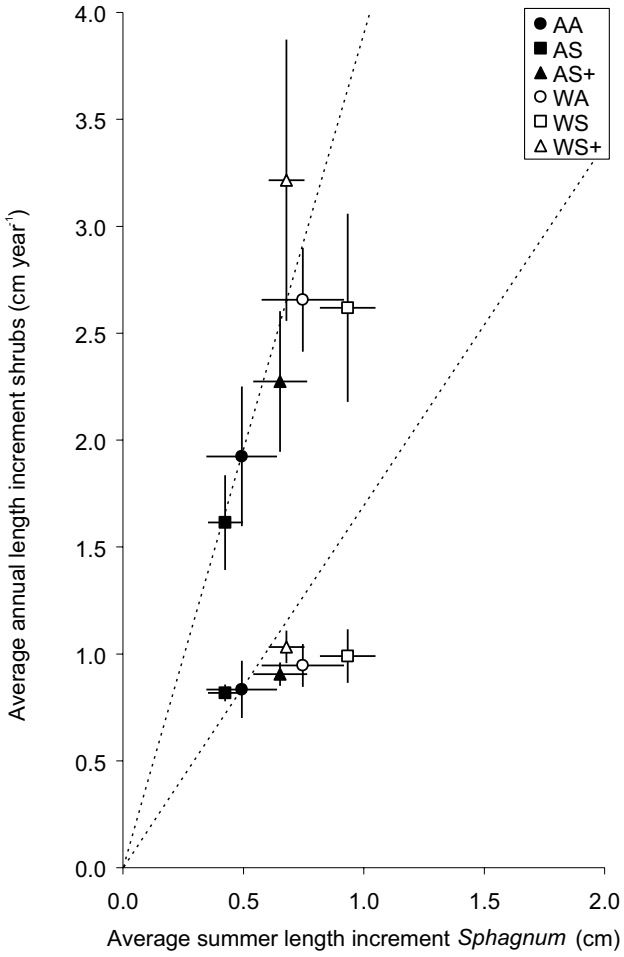

Fig. 2 Average annual apical stem length increment of *Empetrum nigrum* (lower group of points) and average current-year apical stem length of *Betula nana* (upper group of points), relative to average summer length increment of *Sphagnum fuscum* in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) (mean ± SEM, n = 5). The dotted lines indicate ratios of shrub length growth to *Sphagnum* growth equal to the AA treatment of either of the shrub species. All points of a shrub species below the corresponding line showed a relatively smaller response to the treatment than *Sphagnum*. For treatment codes, see Table 1.

year parts of the shoots showed a significant, positive response to the winter treatments, in particular to higher spring temperatures (Tukey HSD: AS +/WS + versus AS/WS: $P < 0.01$). The parts of the shoots that had been formed in the previous year produced more leaf litter in response to summer warming in 2001, but not in 2002 (Table 2). In contrast, the leaf litter production of the older, and lowest parts of the *Betula* shoots, which represented 50-80% of the total leaf litter production, showed a strong, negative response to the summer warming

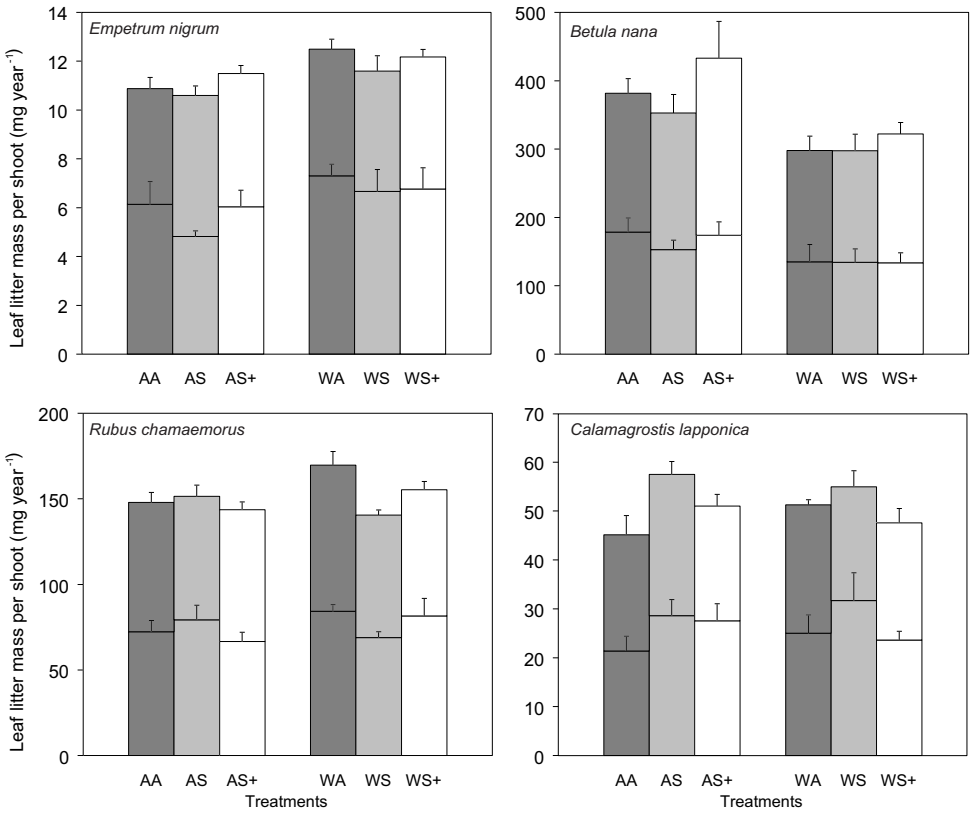

Fig. 3 Annual leaf litter production of *Empetrum nigrum*, *Betula nana*, *Rubus chamaemorus* and *Calamagrostis lapponica* in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming). Indicated are mean + SEM (n = 5) for each treatment in 2001 (lower part of each bar; July 2001 - July 2002 for *Empetrum nigrum*) and 2002 (upper part of each bar; July 2002 - July 2003 for *Empetrum nigrum*). For treatment codes, see Table 1.

treatments (-38% in 2001, -37% in 2002; Fig. 4, Table 2). The leaf litter production of the older parts of the *Betula* shoots was also negatively related to *Sphagnum* growth (Table 3), as was the stem length of this part of the shoot (2001: Pearson $r = -0.46$, $P < 0.01$; 2002: $r = -0.51$, $P < 0.01$). Analysis of covariance showed, however, that the indirect effect of the summer warming treatments, via enhanced *Sphagnum* growth, on leaf litter production of the older shoot parts of *Betula* was limited compared with the direct climate effect (summer treatments $F = 4.48$, $P < 0.05$; *Sphagnum* growth $F = 1.01$, $P > 0.1$).

In contrast to the two shrubs, leaf litter production of *Rubus* and *Calamagrostis* was not affected by any of the climate manipulations, nor was it related to the length growth of *Sphagnum* (Fig. 3, Tables 2 and 3).

Table 3 Correlation (n = 30) between leaf litter production per shoot of *Empetrum nigrum*, *Betula nana* (total shoot and > 2-year old part of shoot), *Rubus chamaemorus* and *Calamagrostis lapponica*, and *Sphagnum fuscum* length growth (*Sphagnum* data from Dorrepaal et al. 2003)

Species	Period	Correlation coefficient
Empetrum	2001-2002	0.52 **
Empetrum	2002-2003	0.04
Betula total shoot	2001	-0.24
Betula total shoot	2002	-0.29
Betula older part shoot	2001	-0.31 $^{+}$
Betula older part shoot	2002	-0.48 **
Rubus	2001	0.10
Rubus	2002	0.03
Calamagrostis	2001	-0.21
Calamagrostis	2002	0.27

$^{+}$ P < 0.1; ** P < 0.01.

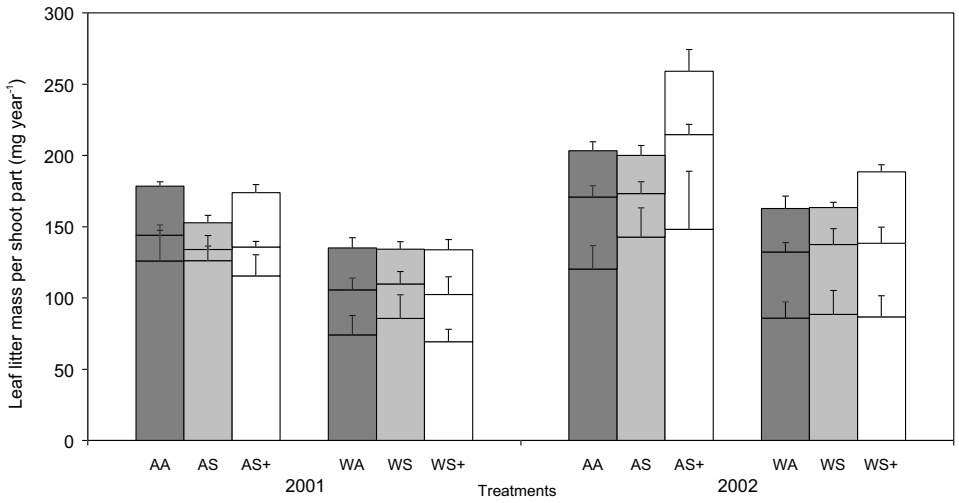

Fig. 4 Annual leaf litter production (mean + SEM, n = 5) of *Betula nana* current-year (upper part of each bar), previous-year (middle part of each bar) and older shoot parts (lower part of each bar) in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) in 2001 and 2002. For treatment codes, see Table 1.

Table 4 Leaf litter N concentration and total shoot N losses through leaf senescence (mean ± SEM, n = 5) of *Empetrum nigrum* (2002-2003), *Betula nana*, *Rubus chamaemorus* and *Calamagrostis lapponica* (2002) in response to summer (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming)

Variable and treatment	*Empetrum*	*Betula*	*Rubus*	*Calamagrostis*
N concentration	(mg/g)	(mg/g)	(mg/g)	(mg/g)
AA	4.3 ± 0.3	5.5 ± 0.3	8.0 ± 0.3	3.8 ± 0.3
AS	3.4 ± 0.1	6.0 ± 0.3	8.2 ± 1.1	4.4 ± 0.3
AS +	3.5 ± 0.1	5.7 ± 0.2	7.6 ± 0.4	4.5 ± 0.2
WA	3.9 ± 0.4	4.9 ± 0.2 **	8.1 ± 1.1	4.3 ± 0.5
WS	4.1 ± 0.2	5.3 ± 0.2 **	6.3 ± 0.2	3.9 ± 0.1
WS +	3.8 ± 0.1	5.1 ± 0.3 **	6.9 ± 0.5	3.9 ± 0.2
N loss	(µg/shoot)	(mg/shoot)	(mg/shoot)	(mg/shoot)
AA	20.2 ± 1.8	1.12 ± 0.12	0.60 ± 0.05	0.09 ± 0.02
AS	19.8 ± 1.4	1.21 ± 0.19	0.57 ± 0.06	0.13 ± 0.01
AS +	19.4 ± 1.3	1.45 ± 0.29	0.58 ± 0.04	0.11 ± 0.01
WA	20.1 ± 1.8	0.80 ± 0.12 *	0.71 ± 0.14	0.11 ± 0.01
WS	19.9 ± 2.7	0.86 ± 0.13 *	0.45 ± 0.03	0.09 ± 0.01
WS +	20.3 ± 1.1	0.96 ± 0.10 *	0.51 ± 0.06	0.09 ± 0.01

Note the different unit for N loss per shoot for *Empetrum*. For treatment codes, see Table 1. Asterisks indicate significance level of differences of variable values compared to values of the same variable without asterisks within the same column (two-way ANOVA): * $P < 0.05$; ** $P < 0.01$.

Leaf litter N losses

By the end of the third summer of the experiment (2002), summer warming appeared to have reduced the leaf litter N concentrations, but this effect was only significant for *Betula* (Table 4). In combination with the negative effects of summer warming on leaf litter production, this reduced the total N losses of *Betula* shoots by 31%. The leaf litter N concentrations and total N losses through leaf litter production of the three other growth forms were not significantly affected by summer warming, nor was there a significant effect of the winter treatments on N concentrations or N losses of any of the growth forms (Table 4).

DISCUSSION

To our knowledge, this is the first report of the vegetative responses of vascular peatland plants to realistic and independent climate manipulations inside and outside the growing season, which, moreover, explicitly includes *Sphagnum*-growth mediated effects. The role of mosses as modifiers of climate change effects on vascular plant communities has been

largely overlooked so far. Our results showed that experimental manipulation of summer and winter climate in a sub-arctic bog had several strong effects on two shrubs, but not on a forb and a grass. Increased *Sphagnum* growth in response to summer warming, however, counteracted several of the potentially positive effects of higher summer temperatures and thicker winter snow cover on those shrubs.

Direct and Sphagnum-*mediated effects of summer warming on growth, leaf litter production and N losses*

The species of the four growth forms investigated here responded differently to the climate manipulations. Relatively small increases in summer temperatures enhanced the apical stem growth of the deciduous shrub *Betula* by up to 50%. This is high compared to the responses of most deciduous shrubs in other studies (Parsons et al. 1994, Hobbie et al. 1999, Bret-Harte et al. 2002, Kudo & Suzuki 2003). The length growth response of the evergreen shrub *Empetrum* to the summer warming treatments was less than that for *Betula*, and less than that for *Empetrum* and other evergreen shrubs in previous warming experiments (Parsons et al. 1994, Shevtsova et al. 1997, Suzuki & Kudo 2000). Positive growth responses of shrubs to enhanced temperatures strongly increased the total canopy height in a tussock tundra (Chapin & Shaver 1996, Bret-Harte et al. 2001) and a dwarf shrub heath (Press et al. 1998). However, in support of our hypothesis (I), the relative response of *Betula* in our sub-arctic bog was in the same range as or slightly weaker than the response of *Sphagnum fuscum*, while the relative response of *Empetrum* was much weaker (see also Sonesson et al. 2002). In contrast to *Sphagnum*, the length growth of shrubs is not vertical, due to the clear inclination of their stems. It therefore seems unlikely that summer warming in sub-arctic peatlands, despite its positive effects on shrub growth, will increase the height of the vascular canopy above the *Sphagnum* carpet. Short, slow growing shrubs, such as *Empetrum*, may even get bogged down by *Sphagnum* as the summers become warmer.

In contrast to our hypotheses (II) and (III), summer warming effects on leaf litter biomass and N losses differed among the growth forms, were negative or neutral, and were only marginally affected by changes in *Sphagnum* growth. For the two shrubs, the small to moderate growth response seemed to play an important role in those effects. The summer warming treatments caused a strong reduction in leaf litter production of the deciduous shrub *Betula*, by reducing the number of leaves per shoot. However, analysis of covariance indicated that *Sphagnum* growth was a less important factor than warming itself. This contrasts with an earlier report, that the presence of living *Sphagnum* significantly reduced the leaf biomass of *Betula*, compared with a *Sphagnum*-removal treatment (Hobbie et al. 1999). In tussock tundra, summer warming enhanced *Betula* leaf production and biomass (Chapin & Shaver 1985, Chapin & Shaver 1996, Hobbie et al. 1999), while it was relatively

unresponsive in a sub-arctic heath (Graglia et al. 1997, Jonasson et al. 1999). Positive responses of aboveground biomass and N-content in warming experiments have been ascribed to increased nutrient acquisition, because of higher mineralisation rates (Chapin et al. 1995, Chapin & Shaver 1996, Rustad et al. 2001), or greater early-season competitive ability of *Betula* for nutrients, owing to advanced leaf phenology (Hobbie & Chapin, 1998). The summer warming treatments in our experiment did not affect *Betula* leaf phenology (S. Berg & E. Dorrepaal, unpublished results), and reduced its leaf litter N concentrations. This suggests that summer warming did not substantially enhance N availability. The increase in apical stem growth of *Betula* in response to summer warming therefore seems to have reduced the growth and maintenance of older shoot parts and short shoots (Chapin & Shaver 1996, Bret-Harte et al. 2001), and reduced the allocation to leaves compared to stems (Parsons et al. 1994).

For the evergreen shrub *Empetrum*, the length of the stems covered with brown leaves was positively related to *Sphagnum* growth, which confirms earlier reports that overgrowth of basal leaves is a major cause of leaf senescence for small evergreen shrubs in peatlands (Backéus 1985). However, increased overgrowth by *Sphagnum* only initially enhanced total leaf litter losses of *Empetrum*. The leaf life-span of *Empetrum* at our site (2.4 years; calculated as the ratio of the length of the harvested stem covered with green leaves to the length covered with senesced leaves) suggests that this regarded leaves that had actually been produced before the start of the experiment. In the third year, leaf litter production in the summer warming treatments was reduced to the ambient level, because enhanced stem elongation had reduced the number of leaves per stem length (data not shown). The distance between leaves on *Empetrum* shoots is known to vary (Mentz 1921, Bell & Tallis 1973). It may increase upon enhanced length growth, because a considerable part of the new shoot is produced from pre-formed winter buds without cell division (Bell & Tallis 1973, Backéus 1985). The length growth response of *Empetrum* to increased summer temperatures may therefore have been limited, but was crucial in avoiding negative impacts of enhanced *Sphagnum* growth on leaf mass and nutrient losses.

In accordance with our hypothesis (III), leaf litter biomass of the forb *Rubus* and the graminoid *Calamagrostis* was not related to *Sphagnum* growth. However, in contrast to hypothesis (II), they did not show direct responses to summer warming either. Aboveground biomass and production responses of graminoids and forbs to experimental warming vary considerably among studies, and may be more related to the effects of higher temperatures on nutrient or light availability (Parsons et al. 1995, Press et al. 1998, Shaver et al. 1998, Jonasson et al. 1999). We did not observe that summer warming had closed the low and open vascular plant canopy in our site, nor did the treatment seem to have increased the

nutrient availability substantially. This may have contributed to the lack of response of *Rubus* and *Calamagrostis*.

Responses of vascular plants to changes in winter and spring climate

Changes in winter snow cover and higher winter and spring temperatures had few effects on the four species of the growth forms investigated in this study. Our hypothesis (IV), that a thicker snow cover would enhance the growth of taller shrubs, such as *Betula*, by protecting their apical shoots and buds, was not supported by our data. Winter mortality of the apical part of the main axis or a secondary long shoot was positively associated with the stem length of *Betula* shoots, but not significantly related to any of the treatments (data not shown). The passive accumulation of snow in the OTCs doubled the snow cover, up to an average thickness of 29 cm in late winter (Dorrepaal et al. 2003). This is both in the range of climate change projections (Maxwell 1992, Houghton et al. 2001, McCarthy et al. 2001), and in the range of the positive relation between snow height and *Betula* shrub height under natural conditions (Sonesson 1969). The relatively small length of the *Betula* main axes (11.1 cm on average) and the low frequency of apical shoot mortality (8.6%) suggest, however, that more than 70% of all shoots must already have been covered by the shallow, 13-cm thick ambient snow cover in the coldest part of the winter (February - April; cf. Dorrepaal et al. 2003, and Aerts et al. 2004). This may explain the lack of winter treatment effects on shoot growth and mortality. The height of the shrub canopy has been shown to increase in response to summer warming (Chapin & Shaver 1996, Press et al. 1998, Bret-Harte et al. 2001), and this effect has been stronger where the ambient snow cover is deep enough to protect the canopy during winter, than in places with a shallow snow cover (Van Wijk et al. 2003). However, even though higher summer temperatures enhanced the length growth of *Betula* in our experiment as well, the increased overgrowth of the stem bases owing to the continuously rising *Sphagnum* surface are likely to counteract increases in the height of the canopy, as explained above. *Sphagnum* may thus prevent positive interactions between summer warming and increased winter snow cover on vascular canopy height and litter production.

Higher spring temperatures, in addition to the increased snow cover, did not significantly affect shrub growth or total leaf litter production of any of the growth forms either. The treatment enhanced the production of leaf litter on the current-year parts of the *Betula* shoots compared to snow addition alone, which indicates that spring warming stimulated the development of the apical leaves and part of the buds. However, on a total shoot basis, the growth, leaf and litter production were not affected. Because leaf phenology was also not (*Betula* and *Calamagrostis*) or only slightly (*Rubus*) affected by our spring warming treatments (S. Berg & E. Dorrepaal, unpublished results), it remains unclear

how much enhanced leaf phenology might contribute to total leaf and litter production. So far, it seems that, even though growth and development of some species or shoot parts may be temperature-limited early in the season, limitations by nutrients or other resources later in the summer (Chapin & Shaver 1996) prevent positive effects of increased spring temperatures on whole shoot growth and production.

Climate change implications for plant interactions in sub-arctic peatlands

Experimental manipulation of summer temperatures has been shown to affect the interactions between vascular and non-vascular plants in various arctic and sub-arctic ecosystems. Declines in moss and lichen production and cover in tussock tundra and dwarf shrub heath have been ascribed to reductions in light availability, due to increased vascular aboveground biomass and litter (Chapin et al. 1995, Press et al. 1998, Hobbie et al. 1999, Cornelissen et al. 2001). However, if the vascular vegetation is low and open, such as on fell-fields, wet sedge tundra and ombrotrophic bogs, and moisture conditions are not negatively affected, increased temperatures may enhance moss performance (Callaghan et al. 1997, Shaver et al. 1998, Jonasson et al. 1999, Sonesson et al. 2002, Dorrepaal et al. 2003, Van Wijk et al. 2003). Although mosses usually inhabit the bottom-layer of the vegetation, their presence and performance has been shown to affect vascular plants as well, through their effects on moisture and nutrient availability, temperature regime and even light availability through overgrowth of stems, leaves or whole plants (Backéus 1985, Sohlberg & Bliss 1987, Hobbie et al. 1999, Ohlson et al. 2001, Limpens et al. 2003).

Our results indicate that summer warming-enhanced *Sphagnum* growth is likely to have a negative impact on shrubs, through the consequences of stem overgrowth for shrub height and functional loss of aboveground stem tissue, but not for leaf litter and N losses. Climate warming itself, however, determines the ability of woody species to cope with the enhanced stem overgrowth, for which there seems to be a trade-off between resource investments in stem or leaf tissue. Increased *Sphagnum* growth may thus directly threaten the survival of *Empetrum*, because of its weak growth response and short total shoot length (2.0 cm on average). *Betula*, which is known as a shrub with a relatively high plasticity of shoot allocation (Bret-Harte et al. 2001), might be able to keep pace with the increasing *Sphagnum* height, but the resulting reduction in the size of its photosynthetic apparatus is likely to hamper its future performance as well. In contrast, *Calamagrostis* (graminoid) and *Rubus* (forb) were neither affected by *Sphagnum* growth, nor by enhanced temperatures. These effects of changes in *Sphagnum* growth on woody versus herbaceous species correspond to previous reported responses of growth and survival of *Betula pubescens* versus *Molinia caerulea* seedlings (Limpens et al. 2003) and *Drosera rotundifolia* plants (Svensson et al. 1995) in relation to N-fertilisation effects on *Sphagnum* growth.

Deciduous and evergreen shrubs are important components of the vascular vegetation of peatlands, particularly bogs (Backéus 1985), and represent 80% of the vascular aboveground biomass at our site (S. Bokhorst & J.H.C. Cornelissen, unpublished results). The structure and stability of moss and peat layers produced by hummock-forming species, such as *Sphagnum fuscum*, largely depend upon the support of overgrown shrub stems (Malmer et al. 1994, Ohlson & Dahlberg 1991). Decreased relative performance of shrubs, due to direct and *Sphagnum*-mediated effects of climate change, may therefore not only alter the vascular plant community, but also affect the stability and functioning of the whole peat-forming system.

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CHAPTER 4

ARE GROWTH FORMS CONSISTENT PREDICTORS OF LEAF LITTER QUALITY AND DECOMPOSABILITY ACROSS PEATLANDS ALONG A LATITUDINAL GRADIENT?

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SUMMARY

1 Plant growth forms are widely used to predict the effects of environmental changes, such as climate warming and increased nitrogen deposition, on plant communities, and the consequences of species shifts for carbon and nutrient cycling. We investigated (I) whether this species-independent classification results in a consistent prediction of patterns in litter quality and decomposition, independent of the environmental conditions; and (II) whether growth forms are as good at predicting decomposability as litter chemistry.

2 We used a natural, latitudinal gradient in NW-Europe as a spatial analogue for future increases in temperature as well as nitrogen availability. Our multi-species (70) screening on *Sphagnum*-dominated peatlands showed that leaf litters of *Sphagnum* mosses, evergreen and deciduous shrubs, graminoids and forbs differed significantly in litter chemistry (total N, P, soluble phenolics, C and lignin concentrations, and phenol/N, phenol/P, C/N, C/P, lignin/N and lignin/P ratios) and that the patterns among groups were independent of the

regional environmental conditions for all variables. Differences in litter chemistry among growth forms were usually larger than differences related to the environmental gradient.

3 After 8 and 20 months incubation of the same litters in outdoor, *Sphagnum*-based decomposition beds, growth forms mostly differed in decomposability as well, but these patterns varied with latitude. *Sphagnum* litters decomposed slower than other litters in all regions, again explaining its high representation in organic deposits of peatlands. Forb litters generally decomposed fastest, while the differences among the other growth forms were small, particularly at higher latitudes.

4 Multiple regression analyses showed that growth forms were better at predicting leaf litter decomposition than chemical variables in warm-temperate peatlands with a high N-load, but less so in the sub-arctic, low-N region.

5 Our results indicate that (I) changes in the relative abundance of growth forms in response to environmental changes may be more important than large environmental changes themselves in determining ecosystem leaf litter chemistry. However, (II) climatic and nutritional constraints in high-latitude peatlands promote convergence towards nutrient-efficient plant traits, resulting in similar decomposition rates of vascular growth forms at different levels and combinations of litter chemistry variables.

INTRODUCTION

Changes in climate due to increasing concentrations of greenhouse gases are expected to be most pronounced at northern high latitudes (Houghton et al. 2001). Sub-arctic and boreal peatlands contain about one-third of the total world soil carbon pool and have acted as a long-term carbon sink, currently estimated to take up 0.07 Pg carbon per year (Gorham 1991, Clymo et al. 1998). Increases in temperatures, subsequent increases in nutrient availability (Rustad et al. 2001), or changes in precipitation may alter the balance between carbon uptake and release through changes in biomass production and decay, which may have important consequences for the global atmospheric carbon balance. Decomposition of dead organic matter regulates the release of nutrients for plant growth as well as the release of carbon into the atmosphere. It is therefore a key process in the responses and feedback of northern peatlands to climate change.

The rate of decomposition processes is related to temperature and moisture or nutrient availability directly (Robinson et al. 1995, Hobbie 1996, Aerts 1997, Ågren et al. 2001, Liski et al. 2003), but also indirectly through their effects on litter quality (Fig. 1, relations 1 and 2; Coulson & Butterfield 1978, Robinson et al. 1995, Aerts 1997, Shaw & Harte 2001). Both experimental warming and increased nutrient availability have been shown to affect litter N and P concentrations, C/N and C/P ratios, carbon, lignin and phenolic

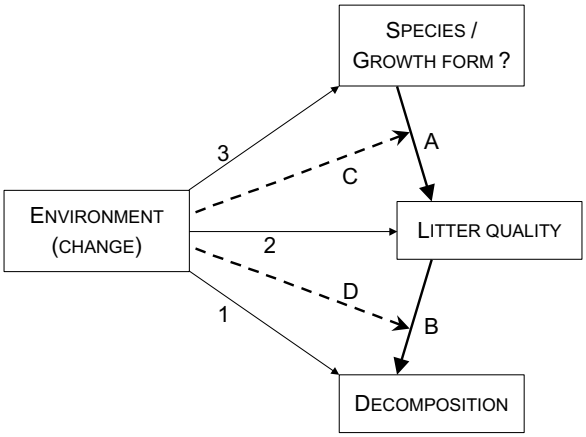

Fig. 1 Diagram indicating several ways in which changes in environmental conditions may affect decomposition. Environment may affect decomposition directly (1), but also indirectly through changes in litter chemistry (2) and shifts in community composition (3). In our study we investigated whether five common peatland growth forms differ in litter quality (A) and decomposability (B), and whether climate or nutrient availability interact with those patterns among the growth forms (C, D).

concentrations (Graglia et al. 2001, Shaw & Harte 2001, Dormann & Woodin 2002, Van Heerwaarden et al. 2003), although the responses of litter chemistry to environmental changes may vary among individual species (Aerts & De Caluwe 1997). At the ecosystem level, however, changes in climate and nutrient availability may also affect decomposition indirectly through changes in community composition (Fig. 1, relation 3). Experimental warming or fertilisation of northern peatlands and heaths has been shown to induce strong shifts in species abundance (Chapin et al. 1995, Press et al. 1998, Weltzin et al. 2003). Plant species in peatlands clearly differ in their decomposition rates (Coulson & Butterfield 1978), and the consequences of species shifts for decomposition at an ecosystem level may be as strong as direct temperature effects (Hobbie 1996, Shaw & Harte 2001).

In order to compare and predict the plant community responses to changes in environmental conditions, it has become customary to classify species into functional groups (Gitay & Noble 1997, Arft et al. 1999, Dormann & Woodin 2002). One of the most frequently used classifications in cool and cold biomes is based on plant growth forms (Chapin et al. 1996). This hierarchical model distinguishes trees, deciduous shrubs, evergreen shrubs, sedges, grasses, forbs, *Sphagnum* mosses, non-*Sphagnum* mosses and lichens, based on differences in their maximum height, responses to temperature, access to moisture and nutrients, the length of their photosynthetically active period and their effects on albedo, carbon gain, decomposition and methane emission. Cluster analysis of 37 tundra species based on traits that were expected to influence ecosystem processes, including responses to climate, resource acquisition rates, and factors affecting nutrient

use, resulted in a similar classification (Chapin et al. 1996). It therefore seems likely that growth-form based functional groups can be a useful tool in predicting the responses of ecosystems to changes in climate or nutrient availability. To be useful for this purpose, however, growth forms are required to show consistent and climate and nutrient availability independent differences in their effects on ecosystem properties, such as litter chemistry and decomposition.

Screenings of large numbers of species from a range of ecosystem types showed that growth forms indeed account for part of the variability in leaf litter decomposability (Cornelissen 1996, Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2000, Quested et al. 2003). However, in a single ecosystem type all species are essentially constrained by the same environmental conditions, which may reduce both the diversity and the number of species and growth forms in its vegetation compared to a range of different ecosystem types. Plant growth in many high-latitude and peatland ecosystems, for example, is strongly nutrient limited, and mature leaf N and P concentrations are lower in peatlands than in other terrestrial ecosystems for all growth forms (Aerts et al. 1999). The low nutrient availability in peatlands and other high-latitude ecosystems may thus decrease or even obscure differences in litter chemistry and decomposition among the growth forms. It therefore remains to be tested whether consistent relations between growth forms, litter quality and decomposability can also be observed within single ecosystem types (Fig. 1, relations A and B). Furthermore, individual species within growth forms have been shown to respond differently to experimental warming or fertilisation, both in litter chemistry (Shaw & Harte 2001, Van Heerwaarden et al. 2003), and decomposability (Robinson et al. 1995, Hobbie 1996). It is therefore not clear whether the patterns of leaf litter chemistry and decomposability among the growth forms (the ranking of the growth forms according to a chemical variable or decomposition rate) are independent of environmental conditions (Fig. 1, interactions C and D).

In this study we therefore investigated the consistency of the patterns in leaf litter chemistry and decomposability among growth forms in three regions along a latitudinal gradient in NW-Europe (52°-68° N), as a spatial analogue for environmental change. We confined ourselves to peatland ecosystems and selected 70 species of the growth forms that are most commonly encountered in those systems, viz. evergreen shrubs, deciduous shrubs, forbs, graminoids and *Sphagnum* mosses. This way we included both direct and indirect effects of changes in climate and nutrient availability, through differences in growing conditions (temperature, precipitation, nitrogen deposition), changes in species composition (within the growth forms) and differences in decomposition conditions (climate, decomposer community). We hypothesised (1) that the differences in litter chemistry and decomposability among growth forms are present within peatlands, although

they may be small, and (2) that the patterns among the groups are not affected by differences in climate or nutrient availability. For several decades, leaf litter decomposability has been related quite successfully to initial 'bulk' litter chemistry, such as total N, P, C, phenol and lignin concentrations and various of their ratios (Coulson & Butterfield 1978, Swift et al. 1979, Melillo et al. 1982, Hobbie 1996, Aerts & Chapin 2000, Pérez-Harguindeguy et al. 2000, Aerts et al. 2003). Since growth forms differ in both nutrient and carbon uptake and allocation strategies, we further hypothesised (3) that growth forms are as good at predicting decomposability as a set of those frequently used litter chemistry variables.

METHODS

Study areas and species

We compared leaf litter quality and decomposability in three regions along a latitudinal gradient in NW-Europe, ranging from 68° N in the north to 52° N in the south (Fig. 2). For brevity, we will indicate the regions in the results and discussion sections primarily as sub-arctic (north Sweden), cool-temperate (south Sweden) and warm-temperate (the Netherlands and Belgium), although we acknowledge that the gradient is characterised by strong differences in temperature and precipitation, as well as in nitrogen deposition (Table 1). The mean annual temperature ranges from -0.5 °C in the sub-arctic to 9.8 °C in the warm-temperate region. The difference in mean winter temperatures is even larger. The annual precipitation-sum more than doubles along the gradient from north to south. These climatic differences are accompanied by an almost tenfold increase in total nitrogen deposition (Table 1).

Table 1 Environmental variables for the three regions where leaf litters were collected and incubated

	Region		
Variable	Sub-arctic	Cool-temperate	Warm-temperate
Mean annual temperature (°C)	-0.5 [a]	7.1 [c]	9.8 [d]
Mean summer temperature (°C)	6.4 [a]	13.0 [c]	14.4 [d]
Mean winter temperature (°C)	-7.4 [a]	1.1 [c]	5.2 [d]
Annual precipitation (mm)	323 [a]	716 [c]	780 [d]
N-deposition 2000 (kg ha^{-1} yr^{-1})	3-5 [b]	10-15 [b]	34 [e]

Temperature and precipitation data are 30-year averages. Summer temperatures refer to May-October, winter temperatures to November-April. a Abisko weather station (Tuomenvirta et al. 2001); b Data provided by the Swedish Meteorological and Hydrological Institute (2003); c Ljungby and Lund weather stations (averaged) (SMHI 2002); d Schiphol weather station (KNMI 2002); e RIVM (2002)

Fig. 2 Map of NW-Europe, indicating the latitudinal gradient with the experimental regions in the sub-arctic (Abisko), in the cool-temperate region (Småland and Lund), and in the warm-temperate region (Amsterdam), where the leaf litters were both collected and incubated.

In each region we collected leaf litter from several *Sphagnum*-dominated peatlands, comprising a broadly similar representation of minerotrophic fens and bog margins as well as strictly ombrotrophic bogs. In north Sweden we collected leaf material at the Stordalen mire and several other peatlands near Abisko (68°21' N, 18°49' E). This litter was incubated in Abisko. In south Sweden we collected leaves on Store Mosse, Dala Mosse, Kopparåsmyren, Åkhultmyren and Björnekulla in the province of Småland (57°07' N, 14°30' E), and incubated those, for practical reasons, in Lund (55°42' N, 13°12' E). In the Netherlands and Belgium we included material from Het Guisveld, De Amstelveense Poel and De Westbroekse Zodden near Amsterdam (52°21' N, 4°55' E), from De Grote Peel in the south of the Netherlands and from Fagne Wallone in Belgium. All this material was

incubated in Amsterdam. In each region, we selected five species per growth form. Those species were generally typical for, and mostly abundant in, the *Sphagnum*-dominated peatlands in each region. The range of included species and families was chosen as broad as possible. We avoided selecting species in more than one climatic region or selecting two species per vascular plant genus in the same region, unless no other species were available. The monocots *Iris pseudacorus* and *Narthecium ossifragum* were classified as forbs (i.e. broad-leaf herbs) based on their broad (non-graminoid) leaves. A list of all species included in the three different regions is given in the appendix.

Litter preparation

Recently senesced leaves were collected in September 2000 around Abisko, in October 2000 in Småland and in November 2000 in The Netherlands and Belgium, following the criteria as described by Cornelissen (1996). Laminas and stalks of compound leaves were both included when they fell off as a unit. This was not the case for *Filipendula ulmaria* and *Sorbus aucuparia* and only the laminas were used. For the collection of *Sphagnum*-litter, *Sphagnum* sods were cut in the field and stored at 4 °C until further use. All *Sphagnum* shoots were separated into three parts: the upper, green and living part of the shoot; the lowest part, which was dark brown and showed clear signs of disintegration; and the middle part, which was usually light brown and had a fresh and coherent structure. This middle part was used as litter, after it had been frozen briefly in liquid nitrogen to ensure its death before the incubation. Leaf litter material of one species of each vascular growth form was frozen in liquid nitrogen too and used as a control. *Sphagnum fuscum* litter was also incubated without being frozen first, as a further test of possible freezing artefacts.

Samples of 1.0 ± 0.05 g air-dried litter were weighed to the nearest mg and sealed into tube-shaped bags made of 0.9-mm-mesh polyester net. Samples of 0.5 ± 0.03 g were used when leaf litter amount was limiting. Bags of 0.3-mm-mesh polyester were used for very small leaves, needles and fine graminoid leaves. As controls, leaf material of 13 species (comprising all growth forms and regions) was incubated as 1.0 g samples as well as 0.5 g samples and leaf material of 12 species (comprising all growth forms and regions) was incubated both in 0.9-mm and in 0.3-mm-mesh bags. In order to standardise the degree of contact among litter pieces, the size of the bags varied between approximately 4 cm x 4 cm and 5 cm x 10 cm, depending on the volume of the leaf material. Breakable leaves of graminoids were cut into 7-cm long pieces and other very large and fragile leaves were cut into halves before weighing. For most species and control treatments we prepared three litterbags per harvest (six in total), but for *Betula pubescens*, *Carex rostrata* and *Empetrum nigrum* there were six litterbags per harvest. For each species, a small litter sub-sample was weighed and oven-dried (70 °C, 48 h) to determine the air-dry mass to oven-dry mass ratio,

in order to calculate the initial oven-dry mass in each litterbag. These sub-samples were subsequently used for the analyses of the initial chemistry.

Incubation

The litterbags were incubated under semi-natural conditions in outdoor *Sphagnum*-based decomposition beds. Each decomposition bed consisted of plastic trays (30 x 40 cm x 15 cm height), containing live, 11-cm thick *Sphagnum* sods. The *Sphagnum* sods in Abisko consisted primarily of *Sphagnum fuscum*. The sods in Lund were cut in Småland and were composed of *S. magellanicum*. In Amsterdam the sods contained primarily *S. palustre* and *S recurvum*. Large holes in the side of the trays, 1.5 cm below the *Sphagnum* surface, allowed for the drainage of excess rainwater, but the bottom was watertight. The experimental design consisted of 12 (Lund, Amsterdam) or 18 (Abisko) trays, which were randomly assigned to three blocks. Within each block half of the trays were assigned to the first harvest and the remaining ones to the second harvest (4 or 6 trays per block). The trays in each block were placed adjacent to each other in experimental gardens in Abisko, Lund and Amsterdam in autumn 2000 and dug 7 cm into the ground to smooth temperature fluctuations.

One litterbag of each species (two for *B. pubescens*, *C. rostrata* and *E. nigrum*) was placed on top of the *Sphagnum*-layer for each block of trays and each harvest date in Lund (9 February 2001), Abisko (11 February) and Amsterdam (21 February). In Abisko a 15-cm thick snow layer was removed first. The litterbags were re-moistened with de-mineralised water in Lund and Amsterdam, but not in Abisko, so as to prevent frost damage. The litterbags were then covered by a 3-cm thick layer of mixtures of leaf-mould of locally abundant peatland species (*Rubus chamaemorus*, *B. pubescens* and *Salix* spp. in Abisko; *Narthecium ossifragum* and *B. pubescens* in Lund; *Phragmites australis*, *Rubus fruticosus* and *Schoenoplectus lacustris* in Amsterdam). The litter layer was secured by a double layer of 3-cm-mesh soft nylon net, which was re-covered by the removed snow in Abisko. During the subsequent summers, we regularly replenished the soil water by adding de-mineralised water below the *Sphagnum* surface, in order to prevent strong drought effects.

We harvested the litterbags after 8 months, on 11 and 20 October and 12 November 2001, and after 20 months, on 8 and 17 October and 7 November 2002, in Abisko, Lund and Amsterdam, respectively, thus including the entire summer seasons of the incubation periods in each region. We removed adhering litter of the cover layer from the outside of the harvested litterbags and removed roots from the litter inside. Upon opening the *Sphagnum* litterbags that were harvested after 20 months, it became clear that not only roots had grown into the bags, but also that partly decomposed fragments of the covering litter layer had entered part of the litterbags and had been caught in the dense, sponge-like structure of the *Sphagnum*. Problems in determining *Sphagnum* mass loss with the litterbag-technique

over periods longer than one year, owing to fine root in-growth or in-washing of material that cannot be removed, are well-recognised (Clymo 1965, Johnson & Damman 1993). We therefore discarded all *Sphagnum* litterbags of the second harvest. From the other litterbags we collected the remaining litter and determined its oven-dry mass (70 °C, 48 h).

Chemical analyses

Because of the large number of species included, we had to confine ourselves to the most frequently used analyses of initial 'bulk' chemical variables of the litters, which have been related to decomposability in many studies (Coulson & Butterfield 1978, Swift et al. 1979, Melillo et al. 1982, Aerts & Chapin 2000, Pérez-Harguindeguy et al. 2000). Initial total nitrogen and carbon concentrations of the litters were determined by dry combustion on a Perkin Elmer 2400 CHNS analyser, and total phosphorus concentration by colorimetry using the ammonium molybdate method (Murphy & Riley 1962), after digestion in 37 % HCl : 65 % HNO_3 (1 : 4, v/v). The total concentration of soluble phenolics was determined by means of the Folin-Ciocalteu method, with tannic acid as a standard (Waterman & Mole 1994). After extraction in 50% MeOH, the phenolic concentration was determined by colorimetry using the Folin-Ciocalteu reagent and aqueous sodium carbonate. Although this method may extract a variety of phenolics, consistent negative relations with nitrogen mineralisation have been found (Palm & Rowland 1997). It may therefore give a crude but meaningful overall indication of the effects of bulk soluble phenolics on decomposition. Initial lignin concentration was determined as described in Poorter & Villar (1997). In brief, after ground, oven-dry plant material has undergone several (polar, non-polar and acid) extraction steps, the mass of the residue, corrected for ash content, and its C and N concentrations are used to calculate the lignin concentration based on the difference in carbon content between cellulose and lignin, after correction for remaining proteins. Although the so-called 'lignin' fraction determined in this and frequently applied other methods (acid-insoluble carbon, Klason lignin) may contain other recalcitrant C-fractions besides true lignin, it has often successfully been used as a litter quality index (Hobbie 1996, Preston et al. 1997 and references therein). For brevity, we will further refer to this fraction as lignin. The initial chemistry values of all litters are given in the appendix.

Data analyses

The percentage litter mass loss (relative to initial dry mass) in all litterbags for each species per harvest were averaged before the statistical analyses to obtain one litter mass loss value per species (see appendix). We first tested whether the differences in mesh size, initial litter mass per bag or treatment with or without liquid nitrogen had affected the mass loss at both harvests. This was generally not the case. No correction of the mass loss data was needed

for the two different starting masses (1.0 versus 0.5 g; paired samples t-test (df = 12) t = 1.41, P = 0.19 (8 months); t = 0.18, P = 0.86 (20 months)) and for the treatment with or without liquid nitrogen (t = 1.70 (df = 3), P = 0.19 (8 months)). However, the mass loss in the fine-mesh litterbags was 5.5 % lower than in the coarse litterbags after 8 months (t = 2.39 (df = 11), P = 0.04), but not after 20 months (t = 1.43 (df = 11), P = 0.18). We therefore corrected the mass loss after 8 months by adding 5.5 % to the percentage mass loss of all species that had been incubated in fine-mesh litterbags.

Initial litter chemistry and mass loss after 8 months were analysed for differences among all five growth forms, among the regions and interactions of growth form and region in separate two-way ANOVAs. Differences in decomposability after 8 and 20 months of incubation among the vascular growth forms, among the regions and their interactions were analysed with a repeated-measures ANOVA (Pillai's trace), with 'incubation time' as within-subject factor and 'growth form' and 'region' as between-subject factors. The repeated-measures ANOVA was followed by separate two-way ANOVAs for each harvest because of a significant interaction of region with incubation time. To compare the potential of the growth forms and litter chemistry variables for predicting decomposability, we used multiple regression analyses, and compared the individual and combined abilities of growth form and litter chemistry to explain the variation in litter decomposition among species. We constructed four 'dummy variables' (Zar 1999) for the factor growth form and two for the factor region. Litter mass loss of all species was then regressed on region alone, or with either or both growth form and chemistry. We selected the best sets of chemical variables for the regression analyses of mass loss after 8 and 20 months, by comparing the predictive power of different combinations of all measured chemical variables or ratios that were not strongly correlated with each other ($r < 0.50$). For mass loss after 8 months, these were total N, P, C and phenol concentrations, while C was replaced by lignin for mass loss after 20 months.

Data were tested for homogeneity of variances with Levene's test. Ln-transformation considerably improved the normality and homogeneity of variances of most of the chemical variables, but not of the C and lignin data or the mass loss data. Mass loss data (fractions) were arcsine-square-root transformed, except when *Sphagnum* mosses were included in the analyses, because of slightly negative mass loss values for three of the *Sphagnum* species in Amsterdam after 8 months. Because analyses of variance and regression analyses are robust to considerable heterogeneity of variances as long as the sample sizes are nearly equal (Zar 1999), we proceeded with the analyses also when homoscedasticity assumptions were not fully met. Post hoc multiple comparisons were included if growth form or region was a significant factor (Tukey HSD or Games-Howell), and those tests were performed

for separate regions if the interaction between the main factors was significant. All analyses were performed with SPSS for Windows 10.1.

RESULTS

Litter chemistry

Leaf litters of the five peatland growth forms differed significantly in initial concentrations of N, P, soluble phenolics, C and lignin, as well as in their most commonly used ratios, phenol/N, phenol/P, C/N, C/P, lignin/N and lignin/P (Table 2, Fig. 3). Total N concentrations were lowest in *Sphagnum* and graminoid litters and highest in forb litters. Soluble phenolic concentrations were highest in evergreen and deciduous shrubs and lowest in *Sphagnum* litters. Total C and lignin concentrations were highest in evergreen shrubs, followed by deciduous shrubs, and were much lower in forbs, graminoids and *Sphagnum* litters. The patterns among growth forms of the C/N and C/P ratios were the opposite of those for total N and P, while the patterns of the phenol/N, phenol/P, lignin/N and lignin/P ratios resembled those of the phenolic and lignin concentrations, respectively (results not shown).

Total N concentrations were significantly lower in leaf litters from the sub-arctic than from both temperate regions (Tukey HSD $P < 0.05$), while total P concentrations were lower in the cool-temperate region than in the other regions (Games-Howell $P < 0.05$). Leaf litters in the cool-temperate region also contained significantly less soluble phenolics than sub-arctic litters (Games-Howell $P < 0.05$), while total C and lignin concentrations did not differ among the regions (Table 2). None of the chemical variables showed significant interactions of growth form with region, indicating that the differences in litter chemistry among growth forms are robust against changes in climate or nutrient availability, and species composition within growth form (Table 2).

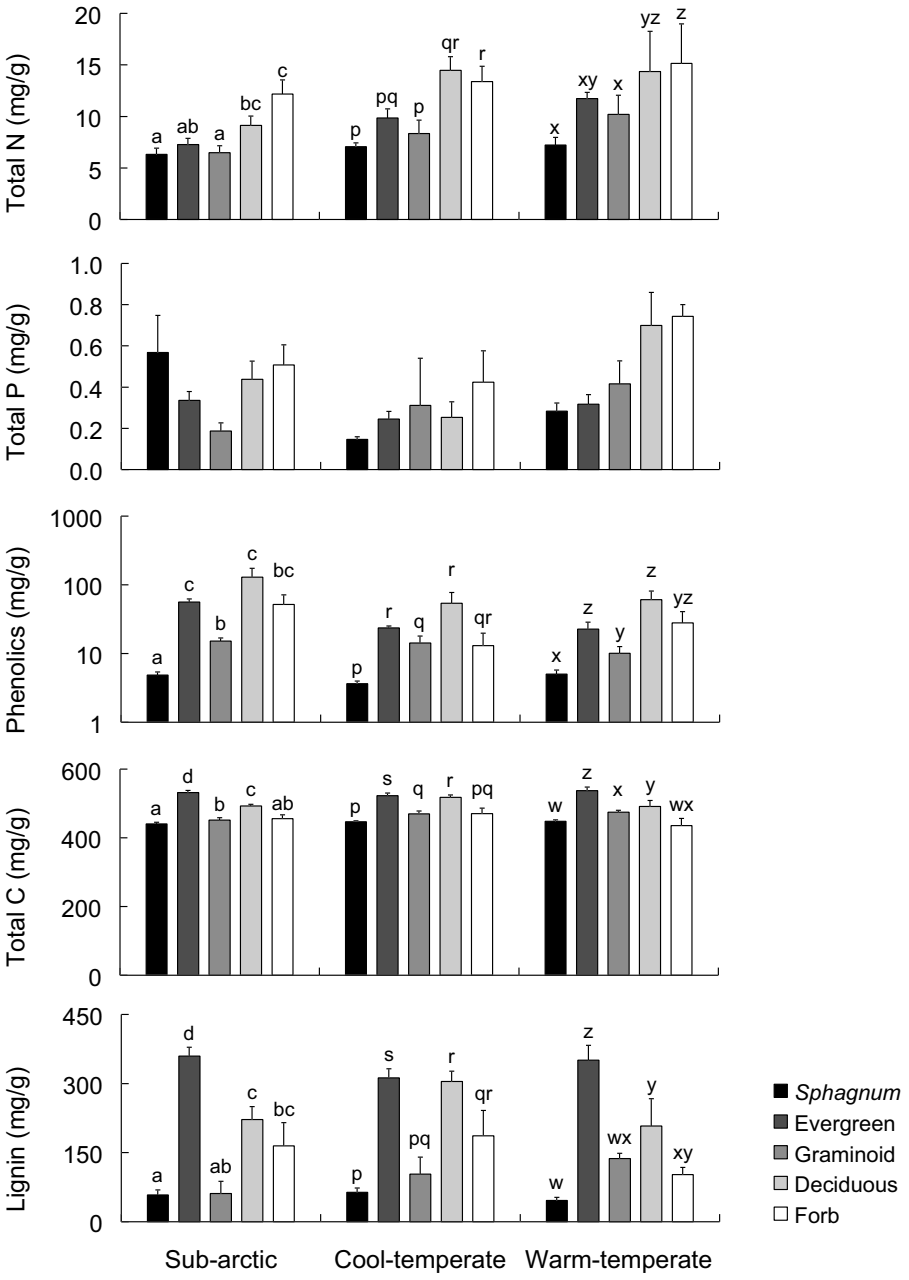

Fig. 3 Initial chemistry (mean + SE) of fresh leaf litters of five different growth forms, collected in three different regions along a latitudinal gradient (n = 5, but n = 4 for *Sphagnum* in the sub-arctic). Note the logarithmic scale of the Y-axis for phenolics. Different letters indicate significant differences ($P < 0.05$) between growth forms within each region (Tukey HSD for total N, Games-Howell for total phenolics, C and lignin).

Table 2 Results of two-way ANOVAS for initial chemistry of fresh leaf litters of five different growth forms (GF), collected in three different regions along a latitudinal gradient (n = 5, but n = 4 for *Sphagnum* in the sub-arctic). Data were ln-transformed before the analyses, except for C, lignin, C/N and lignin/N.

Variable	Source	F	P
N	GF	11.20	< 0.001
	Region	6.67	0.002
	GF × region	0.56	0.81
P	GF	3.61	0.011
	Region	9.65	< 0.001
	GF × region	0.84	0.58
Phenols	GF	27.85	< 0.001
	Region	8.83	< 0.001
	GF × region	1.21	0.31
C	GF	35.33	< 0.001
	Region	1.53	0.23
	GF × region	1.34	0.24
Lignin	GF	38.39	< 0.001
	Region	0.91	0.41
	GF × region	1.46	0.19
Phenol/N ratio	GF	12.37	< 0.001
	Region	11.13	< 0.001
	GF × region	1.14	0.35
Phenol/P ratio	GF	9.69	< 0.001
	Region	3.82	0.028
	GF × region	0.97	0.47
C/N ratio	GF	9.74	< 0.001
	Region	6.73	0.002
	GF × region	0.66	0.73
C/P ratio	GF	3.63	0.010
	Region	9.84	< 0.001
	GF × region	0.86	0.55
Lignin/N ratio	GF	22.97	< 0.001
	Region	3.49	0.037
	GF × region	1.68	0.12
Lignin/P ratio	GF	4.04	0.006
	Region	2.42	0.10
	GF × region	0.66	0.73

Litter decomposability

Litter mass loss after 8 months showed clear differences among five important peatland growth forms (Fig. 4), but the pattern was not consistent across the environmentally different regions, as was shown by the significant interactions between growth form and region (Table 3). *Sphagnum* litter decomposed slowest, while forbs mostly decomposed fastest. The differences in average mass loss among the four vascular growth forms were relatively small, except in the warm-temperate region. Analyses of the 8 and 20-months harvest data of those vascular groups only showed that their patterns in mass loss varied across the regions as well (Table 3, growth form × region P = 0.008), although the interaction was only marginally significant for the separate analysis of the 20-months data (Table 3, growth form × region P = 0.08). The interaction is probably related to the relatively low mass loss of the forbs and deciduous shrubs in the sub-arctic and cool-temperate regions, while these groups decomposed fastest in the warm-temperate region. Moreover, the evergreen shrubs decomposed slowly compared to the other vascular groups, particularly graminoids, in the sub-arctic region, while there were no significant differences in the cool-temperate and warm-temperate regions (Fig. 4).

Table 3 Results of repeated measures ANOVAS and subsequent two-way ANOVAS for percentage mass loss of five peatland growth forms (GF) including *Sphagnum*, or the four vascular growth forms only, collected in three different regions along a latitudinal gradient, after 8 and 20 months incubation in litterbags in *Sphagnum*-based decomposition beds (n = 5, but n = 4 for *Sphagnum* in the sub-arctic). Mass loss data were arcsine-square-root-transformed before the vascular growth forms analyses.

		All growth forms		Vascular growth forms	
Variable	Source	F	P	F	P
Mass loss 8 and 20	Incubation time			48.80	< 0.001
months	Incubation time × GF			0.57	0.64
	Incubation time × region			24.43	< 0.001
	Incubation time × GF × region			1.63	0.16
	GF			8.23	< 0.001
	Region			22.89	< 0.001
	GF × region			3.34	0.008
Mass loss 8 months	GF	34.42	< 0.001	9.86	< 0.001
	Region	35.42	< 0.001	45.42	< 0.001
	GF × region	7.17	< 0.001	4.54	0.001
Mass loss 20 months	GF			5.07	0.004
	Region			6.02	0.005
	GF × region			2.00	0.08

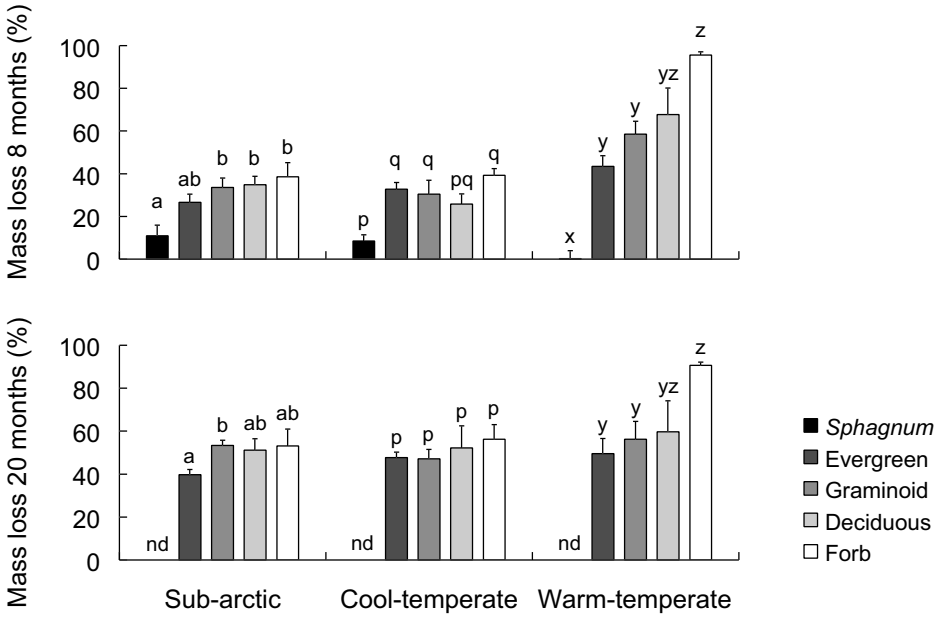

Fig. 4 Percentage mass loss (mean + SE) of leaf litters of five different growth forms, collected in three different regions along a latitudinal gradient (n = 5, but n = 4 for *Sphagnum* in the sub-arctic), after 8 and 20 months incubation in litterbags in *Sphagnum*-based decomposition beds. Different letters indicate significant differences ($P < 0.05$) among growth forms within each region (Tukey HSD for the sub-arctic after 8 months and for the cool-temperate region, Games-Howell for the sub-arctic after 20 months and for the warm-temperate region). nd = not determined.

Growth forms versus litter chemistry

To test whether growth forms were as good at predicting short-term leaf litter decomposability as the most commonly used litter chemistry variables, we added both factors, separately and in combination, to multiple regression models including the data from all regions, or from the separate regions. In the model including the 8-months harvest data from all regions, the addition of growth form increased the explained variance by 44 % from that with region alone, resulting in a fairly good prediction of leaf litter decomposability (total $R^2 = 0.65$, Table 4). In contrast, the initial litter chemistry set (total N, P, soluble phenolics and C concentrations) added only 26 % explained variance to the model (total $R^2 = 0.47$), compared to a model using region only. The combination of both growth from and litter chemistry in the model increased the total R^2 to 0.74. This indicates that the chemical variables contained only 9 % unique information, not covered by the growth forms and region. The growth forms, however, contributed 27 % of unique information to the model, which was not covered by the chemical variables measured in this study.

When *Sphagnum* mosses were excluded, addition of the set of chemical variables to a model including the mass loss data after 8 months in all regions and region as the only

Table 4 Total R^2 of multiple regression models of leaf litter mass loss after 8 and 20 months in litterbags in *Sphagnum*-based decomposition beds, for three different regions along a latitudinal gradient combined or separate. The models included the independent variable 'region' alone (only for all regions combined), or together with either or both of the factors 'growth form' (GF) and 'litter chemistry'. Data sets included species of five peatland growth forms, including *Sphagnum*, or the four vascular growth forms only. Mass loss data were arcsine-square-root-transformed in the vascular growth forms analyses. Litter chemistry included total N, P and phenols for both harvests, total C for the first harvest and lignin for the second harvest. Chemical data were ln-transformed, except for C and lignin. n = 5, but n = 4 for *Sphagnum* in the sub-arctic.

Variables included	All regions		Sub-arctic		Cool-temperate		Warm-temperate	
8 Months (all growth forms)								
Region	0.21***	a						
Region + chemistry	0.47***	b	0.43*	a	0.22	a	0.48**	a
Region + GF	0.65***	b	0.49*	a	0.59**	b	0.84***	b
Region + chemistry + GF	0.74***	c	0.62*	a	0.75**	b	0.88***	b
8 Months (vascular growth forms)								
Region	0.46***	a						
Region + chemistry	0.69***	c	0.32	a	0.39	a	0.58**	a
Region + GF	0.62***	b	0.16	a	0.22	a	0.65**	a
Region + chemistry + GF	0.73***	c	0.46	a	0.53	a	0.72*	a
20 Months (vascular growth forms)								
Region	0.14*	a						
Region + chemistry	0.38***	b	0.54*	b	0.50*	a	0.47*	a
Region + GF	0.31**	b	0.23	a	0.07	a	0.48*	b
Region + chemistry + GF	0.62***	c	0.65*	b	0.79**	b	0.74**	b

Asterisks indicate significance levels of model R^2. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Different letters within the different parts of each column indicate significant changes in R^2 between subsequent levels of each regression model ($P < 0.05$).

factor, increased the R^2 of this model by 0.23 (total $R^2 = 0.69$). Growth form alone was a weaker predictor, only adding 16 % explained variance to the model with region (total $R^2 = 0.62$). The combination of growth form and litter chemistry increased the total R^2 to 0.73, indicating that vascular growth forms contained only 4 % of unique information, while chemistry contained 11 % unique information regarding the variance in leaf litter decomposability (Table 4). After 20 months of incubation, differences in mass loss among the vascular leaf litters was poorly explained by the regions, but the set of chemical variables (including lignin instead of C) improved the total explained variance of the model more, and contained more unique information than growth forms (Table 4), which was comparable to the results after 8 months.

A comparison of the regression models among the three regions showed that the litter chemistry variables in general explained less variation in litter decomposition than the growth forms, when all growth forms were included (Table 4). Furthermore, the percentage of variance explained by growth forms alone increased with decreasing latitude ($R^2 = 0.49$ in the sub-arctic versus $R^2 = 0.84$ in the warm-temperate region). However, when *Sphagnum* was not included as one of the growth forms, the percentage of variance explained by the growth forms decreased considerably in the sub-arctic and cool-temperate regions, both after 8 months and after 20 months (Table 4).

DISCUSSION

This study has provided the first large-scale test of (1) whether growth forms differ in leaf litter chemistry and potential decomposition in a single ecosystem type, viz. peatlands; (2) whether the patterns among growth forms are independent of environmental conditions such as climate or nutrient availability; and (3) whether such a classification of species results in similarly good predictions of litter decomposability as a set of the most widely used explanatory litter chemistry variables. By screening a broad range of species along a latitudinal gradient, we have shown several consistent patterns, but we have also found some interactions with regional climate or nutrient availability. Together these results only partly support the usefulness of the growth form concept.

Environmental and growth-form controls over litter quality

The five growth forms most common in peatlands showed distinct differences in leaf litter chemistry, and the patterns among the growth forms were consistent across a range of environmental conditions for all measured variables. As in other ecosystems (Pérez-Harguindeguy et al. 2000, Shaw & Harte 2001), the total N concentrations of forb litters were higher and C/N ratios, and to some extend C/P ratios, much lower than those of any of the other growth forms. Deciduous shrubs had relatively high N concentrations and low C/N ratios as well, which also confirms previously found patterns (Pérez-Harguindeguy et al. 2000, Shaw & Harte 2001). Forbs tend to dominate vegetation on nutrient-rich sites (Chapin et al. 1996) and are therefore relatively unimportant in terms of cover and biomass production in many nutrient-poor peatlands, especially bogs (Press et al. 1998, Weltzin et al. 2000, Berendse et al. 2001). Although we tried to get equal representation of material from both minerotrophic fens and ombrotrophic bogs for all growth forms, this appeared to be impossible for the forbs, of which most species were collected on fens or relatively minerotrophic margins of large bogs. However, climate warming and subsequent increases in nitrogen availability may increase the biomass of forbs and deciduous shrubs

(Arft et al. 1999, Jonasson et al. 1999), which might result in higher ecosystem litter N concentrations, lower C/N ratios and probably also lower C/P ratios. Total concentrations of soluble phenolics were 13 times higher in leaf litters of deciduous and evergreen shrubs than in *Sphagnum* litters and four times higher than in graminoid litters. Lignin and C concentrations were also highest in the evergreen and deciduous shrubs, thus reflecting the woody nature of those growth forms. Even in a strongly nutrient-limited ecosystem type such as peatlands, growth forms thus differ substantially in bulk litter chemistry (Fig. 1, relation A), and climate or nutrient availability does not interfere with these patterns among growth forms (Fig. 1, interaction C).

Almost all litter chemistry variables and ratios varied in magnitude among the three regions. The consistency in the patterns of litter chemistry among the growth forms makes it unlikely that those differences are caused by the differences in the region-specific species composition used for each growth form, but rather by differences in environmental conditions. N concentrations were lower and C/N ratios higher in the sub-arctic than in both temperate regions, while P concentrations were lower and C/P ratios higher in the cool-temperate region. This is probably the result of a shift from nitrogen-limited growth to phosphorus-limited growth, which has taken place at lower latitudes in Europe owing at least partly to the high anthropogenic nitrogen deposition (Aerts et al. 1992). Greater nitrogen mineralisation due to future climate warming might induce such a shift at higher latitudes as well (Rustad et al. 2001). The double phenolic concentration of leaf litters in the sub-arctic compared to those in both temperate regions may reflect a stronger nutrient limitation on growth in the sub-arctic area. Phenols have been shown to serve as an alternative carbon sink when growth is limited by factors other than C-assimilation (Jones & Hartley 1999, Graglia et al. 2001). Although our multi-species, natural-gradient screening thus suggests that important chemical variables of leaf litters show consistent responses to combined changes in temperature, precipitation and nutrient availability (Fig. 1, relation 2), responses of litter chemistry to experimental fertilisation and particularly to warming vary among species, growth forms and studies (Robinson et al. 1995, Arft et al. 1999, Shaw & Harte 2001, Dormann & Woodin 2002, Van Heerwaarden et al. 2003). Moreover, the variation in litter chemistry among the three regions in our study was usually smaller than the variation among growth forms (Table 2). Changes in the relative abundance of the growth forms may therefore be more important in determining leaf litter chemistry at an ecosystem level than large, long-term changes in temperature, precipitation and nitrogen availability, or shifts in species composition within growth forms.

Environmental, chemical and growth-form controls over decomposition

The hypothesis that growth forms reflect their different nutrient- and carbon-use strategies not only in leaf litter quality, but also in decomposability, even in nutrient-limited peatlands, was supported by our results. However, we also hypothesised that the environmental conditions along a large latitudinal gradient would not interfere with the decomposition patterns among growth forms, which was not supported by our data, as shown by the significant interaction of growth form and region. Forb litters usually decomposed fastest and *Sphagnum* litters slowest, but differences among the other vascular growth forms were generally small, especially at higher latitudes, and patterns were not consistent across regions. These findings correspond to previous screenings of decomposability in peatlands and sub-arctic ecosystems (Verhoeven & Toth 1995, Aerts et al. 1999, Quested et al. 2003), although larger differences among vascular growth forms have been reported for a range of other ecosystems (Cornelissen 1996, Pérez-Harguindeguy et al. 2000). When we compared litter chemistry and growth form as predictive variables for decomposition, the interaction between growth form and environmental region was also apparent. Growth form appeared to be the better predictor when all growth forms were included in the analysis, but the strength of the relation between decomposition and growth form decreased considerably with increasing latitude. This confirms earlier reports that differences in decomposability among growth forms are larger under favourable conditions than in regions with less favourable conditions (Cornelissen et al. 1999), and may indicate that climatic and nutritional constraints for plant growth in peatlands at higher latitudes result in an overall convergence towards stress-tolerant, nutrient-efficient plant traits for all growth forms. Although major growth forms in those regions may show large differences in specific litter quality variables, as we found, the combined effects of several chemical variables probably constrain the leaf litter decomposability in all groups. For instance, decomposition of evergreen and deciduous shrub litters in the sub-arctic may be primarily hampered by the high phenolic, C and lignin concentrations, while graminoid and *Sphagnum* litter decomposition may be restricted by the low N concentrations (Fig. 3). Differences in climatic conditions or nutrient availability thus seem to have different effects on the decomposition of different growth forms, which interferes with the patterns and differences among the groups (Fig. 1, relations A and B, interaction D).

Both chemistry and growth form explained significant proportions of the total variation in decomposition across regions. Growth forms, however, contained a relatively large portion of unique information in relation to decomposition, which was not covered by the selected litter chemistry variables, especially when all growth forms were included (27 % for all regions, up to 40-53 % in the temperate regions). We may thus have missed differentiating chemical or physical information of the leaf litters. Partly because of practical

constraints, we selected the best combination from those chemical variables and ratios that are usually well-correlated with decomposition (Coulson & Butterfield 1978, Swift et al. 1979, Melillo et al. 1982, Hobbie 1996, Aerts & Chapin 2000, Pérez-Harguindeguy et al. 2000, Aerts et al. 2003), and obtained comparable R^2-values, particularly in the warm temperate region or for vascular growth forms only. Lignin/N ratio was not among the selected variables (initial N, P, phenolics and C (8-months harvest) or lignin (20-months harvest) concentrations), although it is often considered to be an important indicator of the decomposability of deciduous and evergreen forest leaf litters (Melillo et al. 1982, Aerts 1997). For wider ranges of growth forms or habitats, however, initial concentrations of lignin, C, N or phenolics, or the C/N or C/P ratios alone may explain as much variation as lignin/N (Coulson & Butterfield 1978, Aerts & Chapin 2000, Pérez-Harguindeguy et al. 2000, Aerts et al. 2003). This may indicate that the factors controlling decomposition differ between woody and non-woody growth forms. It seems more likely that the missing information is related to chemical compounds in *Sphagnum*, with very specific decay-inhibiting effects, such as sphagnan and sphagnum acid (Johnson & Damman 1993, Verhoeven & Toth 1995) or specific phenolic compounds (Swift et al. 1979). Another option would be the physical property leaf tensile strength, which has been shown to explain variation in leaf litter decomposability as well, and is usually high in graminoids and low in forbs (Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2000).

Growth forms and environmental change in northern peatlands

We used a natural, latitudinal gradient, from the sub-arctic to the warm-temperate region, as a spatial analogue for future changes in climate and nutrient availability at higher latitudes, and tested how different growth forms responded in their litter chemistry and litter decomposability. Mean annual temperatures increased by 10.3 °C, while the annual precipitation more than doubled from north to south. Furthermore, our latitudinal gradient was characterised by a tenfold increase in nitrogen deposition from north to south. Over the coming century, arctic and sub-arctic mean summer and winter temperatures are expected to increase by 1.0-8.2 °C and 2.0-14.0 °C, respectively, while precipitation is predicted to increase by 5-80 % (Maxwell 1992, Houghton et al. 2001, McCarthy et al. 2001). Experimental increases in temperature have been shown to stimulate nitrogen mineralisation (Chapin et al. 1995, Hobbie 1996, Robinson 2002), and increased nitrogen availability may therefore be a realistic indirect consequence of climate warming. However, although tenfold increases in N-mineralisation have been observed upon experimental warming (Nadelhoffer et al. 1991), the average increase in a meta-analysis of warming experiments was only 46 % (Rustad et al. 2001). Moreover, the higher temperatures in the more southern regions may also result in higher mineralisation rates, thus increasing

the range in N availability along our gradient even further. The changes in temperature, precipitation and N availability along the latitudinal gradient were therefore in the same direction, but probably larger than can be expected at high latitudes according to realistic global change scenarios.

Other differences among the regions included shifts in the collected plant species and possible changes in the composition and activity of the decomposer community in our decomposition beds, the latter partly because of the differences in the plant species composing the incubation medium. The composition of the decomposer community may vary with both resource quality and climate (Swift et al. 1979), but along climatic gradients this does not seem to affect the ranking of plant species according to their litter decomposability (Cornelissen et al. 1999, González & Seastedt 2001). Changes in climate and nutrient availability have been shown to induce shifts in plant community composition (Chapin et al. 1995, Press et al. 1998, Weltzin et al. 2003). Indeed, it was hard to find five relatively abundant forbs on the peatlands in the sub-arctic, while the same was true for woody evergreen species in the warm-temperate region (E. Dorrepaal, personal observation). Although the actual shifts in the vegetation due to changes in climate or nutrient availability may not be as broad as the differences included in this study, we deliberately chose a wide range of species and equal numbers of species within each growth form, in order to test the true independence of the growth forms from the identities of the actual species they represented, as predictors of litter properties. The highly consistent patterns in leaf litter chemistry we found, indicate that the main differences in litter quality, decomposability and incubation conditions among the three regions were most likely related to direct and indirect effects of differences in temperature, precipitation and nitrogen availability, in other words the key factors in global change scenarios.

Experimental warming of arctic and peatland ecosystems tends to enhance shrubs, but responses of forbs, graminoids, *Sphagnum* and other mosses vary considerably (Arft et al. 1999, Weltzin et al. 2001, Dormann & Woodin 2002, Weltzin et al. 2003, Dorrepaal et al. 2003, Van Wijk et al. 2003). Responses to increased nutrient availability seem to be more straightforward, with usually positive effects on graminoids, positive or no effects on forbs and deciduous and evergreen shrubs, and negative effects on *Sphagnum* mosses (Press et al. 1998, Jonasson et al. 1999, Dormann & Woodin 2002, Van Wijk et al. 2003). Our data suggest that warming and increased nutrient availability may thus increase the ecosystem-level concentrations of phenolic compounds, C and lignin because of shifts towards shrubs, but may also increase litter N concentrations and reduce the C/N ratios because of reduced production of *Sphagnum*, possibly increased production of forb litter, and direct effects on all growth forms. Reduced *Sphagnum* production would strongly increase the overall peatland decomposition rate. However, because of ecological convergence and inconsistent

patterns, the value of growth forms for a reliable translation of changes in vascular growth form abundance and litter chemistry in peatlands to leaf litter decomposability appears to be limited, particularly at higher latitudes.

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Appendix Scientific species names, initial chemistry and mass loss after 8 and 20 months incubation in *Sphagnum*-based decomposition beds for all leaf litters included in the study of leaf litter quality and decomposability in peatlands along a large-scale latitudinal gradient

Species	Region	Growth form	N (mg/g)	P (mg/g)	Phenolics (mg/g)	C (mg/g)	Lignin (mg/g)	Mass loss 8 months (%)	Mass loss 20 months (%)
Sphagnum balticum	SA	S	7.9	0.67	4.8	438	43	9.5	nd
Sphagnum fuscum	SA	S	5.5	0.23	6.3	454	89	4.2	nd
Sphagnum riparium	SA	S	6.6	1.03	3.8	437	41	25.5	nd
Sphagnum warnstorfii	SA	S	5.3	0.34	4.6	433	59	4.5	nd
Andromeda polifolia	SA	E	6.4	0.34	47.4	529	370	27.1	31.0
Empetrum nigrum	SA	E	5.5	0.32	62.9	556	421	33.6	43.6
Juniperus communis	SA	E	8.8	0.48	39.7	523	302	33.4	44.5
Rhododendron lapponicum	SA	E	8.5	0.21	77.2	533	356	26.5	40.4
Vaccinium vitis-idaea	SA	E	7.1	0.34	53.0	516	350	12.6	39.5
Calamagrostis lapponica	SA	G	5.5	0.19	9.8	433	0	45.4	58.1
Carex rotundata	SA	G	8.0	0.28	17.6	445	37	31.5	48.3
Carex vaginata	SA	G	8.2	0.27	19.7	446	33	38.4	51.7
Eriophorum vaginatum	SA	G	4.8	0.12	13.3	472	153	18.3	60.2
Trichophorum cespitosum	SA	G	5.9	0.08	15.3	462	83	34.1	48.3
Arctostaphylos alpinus	SA	D	6.4	0.38	301.6	499	161	45.3	70.1
Betula nana	SA	D	10.6	0.52	89.8	505	278	25.3	40.0
Salix lapponum	SA	D	11.5	0.74	49.2	484	289	28.2	42.5
Salix myrsinites	SA	D	8.6	0.31	86.0	480	158	43.0	53.0
Vaccinium uliginosum	SA	D	8.6	0.24	118.5	495	223	32.4	50.2
Bartsia alpina	SA	F	13.1	0.83	43.4	434	57	49.7	59.4
Bistorta vivipara	SA	F	13.4	0.37	16.2	472	302	30.3	36.3
Rubus chamaemorus	SA	F	13.2	0.63	118.7	481	118	39.4	61.7
Saussurea alpina	SA	F	14.4	0.35	12.2	423	82	54.9	74.6
Saxifraga aizoides	SA	F	6.8	0.35	68.1	468	267	18.5	33.4
Sphagnum angustifolium	CT	S	7.1	0.17	3.8	442	57	18.5	nd
Sphagnum cuspidatum	CT	S	5.7	0.14	2.7	446	52	8.9	nd
Sphagnum magellanicum	CT	S	7.7	0.13	3.4	451	65	5.1	nd
Sphagnum papillosum	CT	S	7.0	0.11	3.5	453	98	1.2	nd
Sphagnum rubellum	CT	S	7.8	0.18	4.8	443	48	8.8	nd
Andromeda polifolia	CT	E	6.7	0.16	27.7	508	327	34.7	45.7
Calluna vulgaris	CT	E	10.7	0.27	18.5	537	354	28.4	41.5
Ledum palustre	CT	E	10.1	0.36	22.3	531	345	23.1	45.0
Picea abies	CT	E	9.9	0.27	26.3	501	249	36.6	49.9
Pinus sylvestris	CT	E	11.9	0.17	23.0	537	285	40.9	56.4
Carex lasiocarpa	CT	G	6.7	0.06	15.7	460	57	34.8	43.7
Carex rostrata	CT	G	13.1	1.22	7.3	444	11	50.4	55.4
Eriophorum angustifolium	CT	G	5.5	0.01	27.9	479	152	14.3	45.7
Molinia caerulea	CT	G	8.3	0.16	9.7	470	80	35.0	57.6
Rhynchospora alba	CT	G	8.1	0.11	10.7	495	219	17.3	33.3

Species	Region	Growth form	N (mg/g)	P (mg/g)	Phenolics (mg/g)	C (mg/g)	Lignin (mg/g)	Mass loss 8 months (%)	Mass loss 20 months (%)
Betula pubescens	CT	D	10.2	0.12	70.5	522	293	35.3	45.9
Myrica gale	CT	D	15.9	0.04	136.9	540	351	13.6	47.8
Salix pentandra	CT	D	16.2	0.29	29.1	520	356	31.5	49.7
Sorbus aucuparia	CT	D	17.3	0.46	3.4	497	237	33.5	90.0
Vaccinium myrtillus	CT	D	12.8	0.35	29.1	510	284	15.2	27.8
Epilobium palustre	CT	F	13.4	0.61	7.3	515	342	28.6	37.5
Filipendula ulmaria	CT	F	17.4	0.40	39.8	434	0	37.1	56.3
Iris pseudacorus	CT	F	8.4	0.17	3.8	438	191	45.1	71.0
Narthecium ossifragum	CT	F	12.6	0.05	3.8	495	228	46.1	71.7
Stachys palustris	CT	F	15.1	0.90	10.5	470	172	39.2	44.7
Sphagnum contortum	WT	S	6.2	0.20	2.3	436	43	-5.0	nd
Sphagnum fallax	WT	S	5.5	0.34	4.8	445	25	13.3	nd
Sphagnum palustre	WT	S	6.5	0.21	6.5	462	57	-5.5	nd
Sphagnum squarrosum	WT	S	9.5	0.40	5.6	447	43	3.8	nd
Sphagnum subnitens	WT	S	8.4	0.26	5.9	449	63	-5.3	nd
Calluna vulgaris	WT	E	12.1	0.19	10.4	537	305	53.8	62.9
Erica tetralix	WT	E	12.4	0.26	18.9	574	445	52.7	66.4
Ledum groenlandicum	WT	E	10.7	0.37	45.6	515	320	30.5	36.4
Pinus sylvestris	WT	E	13.4	0.30	17.3	524	274	47.5	51.2
Vaccinium vitis-idaea	WT	E	10.0	0.47	21.1	538	409	32.7	30.9
Calamagrostis canescens	WT	G	7.9	0.51	4.8	474	132	62.0	69.0
Carex acutiformis	WT	G	12.2	0.64	17.7	485	175	47.8	30.7
Juncus subnodulosus	WT	G	10.0	0.10	4.5	465	113	80.4	67.2
Phragmites australis	WT	G	15.9	0.63	9.0	490	117	48.7	42.4
Schoenoplectus lacustris	WT	G	5.0	0.20	14.2	457	149	53.6	72.1
Alnus glutinosa	WT	D	28.9	0.44	22.6	526	309	28.3	23.4
Aronia x prunifolia	WT	D	5.8	0.56	129.7	467	130	76.4	68.4
Lonicera periclymenum	WT	D	13.5	1.33	43.6	439	81	98.8	87.7
Rubus fruticosus	WT	D	10.4	0.60	83.4	502	132	82.6	90.9
Salix cinerea	WT	D	13.2	0.56	24.9	524	388	52.6	28.0
Angelica sylvestris	WT	F	14.3	0.70	7.4	443	105	96.5	91.5
Caltha palustris	WT	F	30.2	0.92	11.2	463	84	91.2	94.3
Chamerion angustifolium	WT	F	10.9	0.74	77.0	494	162	99.0	92.7
Cirsium palustre	WT	F	10.0	0.79	25.2	403	74	92.9	87.0
Hydrocotyle vulgaris	WT	F	10.3	0.57	19.2	377	87	98.2	88.0

Regions: SA = sub-arctic; CT = cool-temperate; WT = warm-temperate. Growth forms: S = *Sphagnum*; E = woody evergreen; G = graminoid; D = woody deciduous; F = forb. Nomenclature of vascular plant species follows Mossberg et al. (1992) for the sub-arctic and cool-temperate region and Van der Meijden (1996) for the warm-temperate region (Van der Meijden et al. (1983) for *Ledum groenlandicum*). *Sphagnum* nomenclature follows Bouman & Van der Pluijm (2002). Vouchers of the *Sphagnum* species are preserved in the Leiden branch of the Nationaal Herbarium Nederland (L). nd = not determined.

CHAPTER 5

CHANGING LEAF LITTER FEEDBACKS ON PLANT PRODUCTION ACROSS CONTRASTING SUB-ARCTIC PEATLAND GROWTH FORMS

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Submitted

ABSTRACT

Plant species and growth forms differ widely in litter chemistry, which affects decay and may have important consequences for the release of plant available nutrients and growth inhibitory compounds. We investigated the short-term (9.5 months) and medium-term (21.5 months) feedback effects of leaf litter quality and quantity on plant production, and tested whether plant growth forms can be used to generalize interspecific differences.

Leaf litters of 20 sub-arctic vascular peatland species changed clearly over time in their effects on the test plant *Poa alpina*. Across all growth forms, litter reduced plant biomass after 9.5 months, by up to 49 % compared with untreated plants. This effect was strongest for litters with a high decomposition rate or low initial lignin/P ratio. In the second year, however, litter effects on biomass production were neutral or positive, which was related to initial litter N concentration (positive), and C/N, phenol/N and phenol/P ratios (negative), but not to litter decomposability. This indicates that fast initial decay enhanced

microbial or chemical nutrient immobilization and phytotoxicity by phenolic or other carbon compounds, but that nutrient mineralization was stimulated in a later phase.

Differences in effect size among several litter species were large, e.g. plant biomass increase was up to 55 % reduced by *Arctostaphylos alpinus* litter compared with *Saussurea alpina* litter. Differences in response to increasing litter quantities (100, 200 or 300 g m^{-2}) were smaller than or of similar magnitude as differences in response to three contrasting litter species. Growth forms did not differ in litter effects in the first year, but second-year plant production tended ($P < 0.10$) to increase in response to litters of different growth forms, in the order: evergreen shrubs < graminoids or deciduous shrubs < forbs.

Our results indicate that, even within nutrient-constrained ecosystems such as northern peatlands, vascular plant species and possibly growth forms may clearly differ in litter feedbacks to plant growth. However, the long-persisting negative effects of many peatland litters across all growth forms emphasize the importance of growth strategies with a reduced dependence on mineralized nutrients, through efficient conservation or access to alternative nutrient sources.

INTRODUCTION

Decomposition and mineralization of dead organic matter regulate the availability of nutrients for plant growth and are therefore important processes in ecosystems with low external nutrient inputs, such as northern peatlands. Both processes are to a large extent controlled by the chemical composition of the substrate, which may differ considerably among plant species and growth forms (Coulson and Butterfield 1978, Swift et al. 1979, Hobbie 1996, Pérez-Harguindeguy et al. 2000). Nitrogen (N) release has, for example, successfully been related to both litter N concentration and decomposition rate (Berg and Staaf 1981, Quested et al. 2002). However, decomposing litter may not necessarily improve plant growth conditions. N-poor litters may initially reduce N availability as a consequence of microbial immobilization (Berg and Staaf 1981, Melillo et al. 1982, De Jong and Klinkhamer 1985, Van Vuuren 1992, Aerts and De Caluwe 1997), while litters rich in phenolic compounds may inhibit plant growth through their release (Sydes and Grime 1981, Kuiters 1990). The relation between litter quality, decomposability and plant growth conditions is therefore not straightforward, and may change over time.

Because plant species differ considerably in litter quality and decomposability, they may also differ in their litter effects on plant growth (Schlatterer and Tisdale 1969, Ahlgren and Ahlgren 1981, Sydes and Grime 1981, Van Vuuren 1992, Quested et al. 2003b). Growth forms are often used to generalize the role of different plant species in ecosystem functioning and their responses to environmental disturbances such as climate

change (Chapin et al. 1996, Arft et al. 1999, Aerts and Chapin 2000, Dormann and Woodin 2002). Growth forms may differ in litter quality and quantity as well (Cornelissen 1996, Aerts et al. 1999, Pérez-Harguindeguy et al. 2000, Quested et al. 2003a, Dorrepaal et al. in press), and they may therefore be useful in generalizing difference in litter effects on plant growth. Many evergreen shrubs, for example, produce small amounts of N- and P-poor, but phenol- and lignin-rich litter, which decomposes slowly. It has been suggested that the negative effects of these litter properties on nutrient availability may be important for their dominance in nutrient-limited ecosystems, by reducing the competitive ability of more nutrient-demanding, fast-growing species (Berendse 1994, Aerts 1999). Forbs, on the other hand, usually produce N- and P-rich but lignin-poor litters that decompose fast (Pérez-Harguindeguy et al. 2000, Quested et al. 2003a, Dorrepaal et al. in press), and may thus form a positive feedback to nutrient availability. Plant growth forms might also be useful in predicting the feedback of qualitative and quantitative changes in ecosystem litter input, as a consequence of environmental-change induced shifts in plant community composition (Chapin et al. 1995, Press et al. 1998, Arft et al. 1999), to plant growth and ecosystem nutrient cycling (Hobbie 1992, Berendse 1994). However, the small number and widely differing experimental approaches of litter feedback studies performed so far hamper comparisons among growth forms, and obscure the general relations of plant growth with litter quality, decomposability, and quantity through time (Schlatterer and Tisdale 1969, Ahlgren and Ahlgren 1981, Sydes and Grime 1981, Van Vuuren 1992, Xiong and Nilsson 1999, Quested et al. 2003b).

To fill this gap in our knowledge, we investigated how leaf litters of northern peatland species affect plant growth in the short and medium term, through differences in initial chemistry and decomposability, and we explicitly tested whether litter effects differ among plant growth forms. Furthermore, we aimed to compare the relative effects on plant growth of differences in litter quantity compared to differences in litter quality among contrasting litter species. In order to do this, we screened leaf litters of 20 sub-arctic peatland species of four different growth forms, viz. evergreen shrubs, graminoids, deciduous shrubs and forbs, for their effects on plant growth. We added those litters to nutrient-deficient *Poa alpina* test plants and related the plant biomass responses in the first two growing seasons to growth form identity and key chemical variables of the litters. Furthermore, we compared the effects of three different amounts of leaf litter of three contrasting peatland species on plant production.

We hypothesized that (1) plant growth will be positively related to initial litter N and P concentrations and to decomposability, and negatively to litter phenol, C and lignin concentrations, but the strength of those relations may change over time. We therefore also hypothesized that (2) peatland species will vary in their litter effects on plant growth, and

the growth response to leaf litter addition will increase in the order evergreen shrub litters < graminoid or deciduous shrub litters < forb litters. We expected that the effect of litter quantity on plant growth would depend on both nutrient and phenol concentrations of the litter as well, which may vary among peatland species by a factor of three (N) up to 30 (phenols) (Dorrepaal et al. in press). We therefore hypothesized that (3) differences in litter effects on plant growth among contrasting species will be as large as or even larger than differences due to two- to three-fold increases in litter quantity.

METHODS

Phytometer and litter preparation

Poa alpina is a perennial grass that is often viviparous (Mossberg et al. 1992). This allowed us to collect plantlets directly from parent plants in Abisko, north Sweden (68°21' N, 18°49' E), in late July 2000. Four plantlets were planted in each of 289 1-liter pots with a mixture of nutrient-poor peat and sand (1:4 by volume), including some sieved (4-mm mesh) local peat with fine roots to provide an inoculum of natural soil organisms. All *P. alpina* plants (phytometers) were kept in the greenhouse and watered with mineral-poor tap water until early October, when the litter treatments started. At that time we recorded their number of leaves and the length of their longest leaf, we harvested 25 pots and used the dry mass (70 °C, 48 h) of those phytometers to obtain the best estimate for the initial biomass in each pot.

In September 2000, we collected freshly senesced leaves of 21 vascular plant species at several *Sphagnum*-dominated fens and bogs near Abisko, following Cornelissen (1996). All litter material was air dried until further use. Fragile leaves of graminoids were cut into 7-cm pieces.

Fertilizer, litter quantity and growth form experiments

First, we tested the phytometer responsiveness to small increases in nutrient availability. In May and June 2001 and 2002, we applied four amounts of both N (0, 7.5, 15, or 30 mg N pot^{-1} $season^{-1}$ (equivalent to approximately 0, 0.75, 1.5, or 3 g N m^{-2} $season^{-1}$), given as NH_4NO_3) and P fertilizer (0, 1.1, 2.3, or 4.5 mg P pot^{-1} $season^{-1}$ (equivalent to approximately 0, 0.11, 0.23, or 0.45 g P m^{-2} $season^{-1}$), given as KH_2PO_4) in six doses, given weekly. Each treatment was replicated 12 times. The highest dose corresponded to the amount of N in the most nutrient-rich litter in the growth form experiment (*Saussurea alpina*), and an N/P ratio of 7, which was based on previously measured N/P ratios of leaf litters of a subset of the same species (H.M. Quested and J.H.C. Cornelissen, unpublished results).

The litter quantity experiment comprised leaf litters of three contrasting species, having either small, nutrient-poor and phenol- and lignin-rich leaves (*Empetrum nigrum*); broad, nutrient- and phenol-rich leaves (*Potentilla palustris*); or narrow, nutrient-rich and phenol-poor leaves (*Carex rostrata*; see appendix). We added either 1.0, 2.0 or 3.0 ± 0.05 g of each litter species to 12 replicate pots with phytometers (equivalent to approximately 100, 200 or 300 g m^{-2}). The growth-form experiment comprised leaf litters of four vascular growth forms (evergreen shrubs, graminoids, deciduous shrubs and forbs) and five species per growth form (Table 1). Those species were generally typical for, and mostly abundant in, the *Sphagnum*-dominated peatlands in the Abisko area, and the range of genera and families was chosen as broad as possible. For each of those 20 species, we added 2.0 ± 0.05 g litter to each of six replicate pots (equivalent to approximately 200 g m^{-2}). All air-dried litter samples were weighed to the nearest mg and spread out on the soil between and around the four phytometers in early October 2000. This resulted in a litter-layer thickness of approximately 1 mm for small, evergreen leaves, up to 2 cm for larger, curled, forb leaves. Phytometer foliage was not covered by any of the litter types. Each pot was then covered with a double layer of 0.5-cm-mesh, soft nylon net to prevent any litter from entering or leaving the pots.

All pots were transferred to an enclosed, outdoor experimental garden in Abisko, where the treatment replicates were equally distributed over six blocks. Throughout the growing season all pots were watered daily in order to prevent the pots from drying out and to minimize litter effects on soil moisture. We recorded air and soil temperatures (15-min intervals, Axiom SmartReader Plus 8 NTC thermistor probes and dataloggers) in the 1-g and 3-g treatments of the litter quantity experiment during three periods in 2001 (27 June – 6 July, 8 – 14 July and 23 July – 8 August; one replicate per period), to test whether the leaf litters affected soil temperatures. This was not the case: average daily temperatures in the upper 3 cm of soil were not affected by litter amount, nor by differences among the litters of the three contrasting species (two-way ANCOVA: litter amount: $F = 1.82$, $P = 0.21$, species: $F = 2.29$, $P = 0.15$, litter amount × species: $F = 2.09$, $P = 0.17$, covariate (average air temperature): $F = 1280.12$, $P < 0.001$).

Growth measurements

We determined the effects of the different treatments on the peak biomass of the phytometers (end of July, beginning of August) in the first (9.5 months) and the second (21.5 months) growing season. We included all living and senesced vegetative and generative tissues. Therefore, we collected senesced *P. alpina* leaves from each pot throughout both growing seasons, to prevent them from decomposing. Flowering stems and plantlets were collected when they were fully developed but before the plantlets would fall of, or during harvest.

Table 1 Species tested for their litter effects on plant growth in the growth form experiment, and codes used in figures and tables

Growth form	Species	Code
Evergreen shrubs	*Empetrum nigrum*	*En*
	Juniperus communis	*Jc*
	Vaccinium vitis-idaea	*Vv*
	Andromeda polifolia	*Ap*
	Rhododendron lapponicum	*Rl*
Graminoids	*Carex rotundata*	*Cr*
	Calamagrostis lapponica	*Cl*
	Trichophorum cespitosum	*Tc*
	Carex vaginata	*Cv*
	Eriophorum vaginatum	*Ev*
Deciduous shrubs	*Arctostaphylos alpinus*	*Aa*
	Salix myrsinites	*Sm*
	Vaccinium uliginosum	*Vu*
	Salix lapponum	*Sl*
	Betula nana	*Bn*
Forbs	*Bartsia alpina*	*Ba*
	Potentilla palustris	*Pp*
	Saussurea alpina	*Sa*
	Rubus chamaemorus	*Rc*
	Bistorta vivipara	*Bv*

Nomenclature follows Mossberg et al. (1992).

At the first harvest (2001), we recorded the following allometric characteristics of each phytometer in all pots: number of green leaves, length of the longest leaf, number of tillers, and number of flowering stems. We then harvested half of the fertilizer experiment and half of the litter quantity experiment (but none of the growth form experiment), by carefully removing all remaining litter and washing the roots of the phytometers. For all treatments of the growth-form experiment, we estimated the biomass per pot after 9.5 months using their measured allometric traits, and the best equation resulting from simple linear regressions of the biomass of the harvested pots (zero-level fertilization and all litter quantity treatments) on the various allometric traits (biomass = 0.023 * total number of tillers + 0.328, $R^2 = 0.67$, $P < 0.001$, $N = 54$). All remaining plants of the fertilizer and litter quantity experiments and the full growth form experiment were harvested in 2002. The litters were further cleaned

from sand when they were air-dry. Plant parts (including those collected earlier in the season) and litters were oven dried (70 °C, 48 h) and weighed.

Litter analyses

A small sample of air-dried litter of each species was weighed at the same time as the experimental samples and oven-dried (70 °C, 48 h) to determine the air-dry mass to oven-dry mass ratio. We used this ratio to calculate the initial oven-dry mass of the litter in each pot, and calculated litter decomposition as the percentage dry mass loss at harvest. The initial litter samples were also used for the analyses of a set of 'bulk' chemical variables, which have been related to decomposability in many studies (Coulson and Butterfield 1978, Swift et al. 1979, Melillo et al. 1982, Palm and Rowland 1997, Aerts and Chapin 2000, Pérez-Harguindeguy et al. 2000). Initial total N and C concentrations of the litters were determined by dry combustion on a Perkin Elmer 2400 CHNS analyzer, and total P concentration by colorimetry using the ammonium molybdate method (Murphy and Riley 1962), after digestion in 37 % HCl : 65 % HNO_3 (1 : 4, v/v). The total concentration of soluble phenolics was determined by means of the Folin-Ciocalteu method, with tannic acid as a standard (Waterman and Mole 1994). After extraction in 50% MeOH, the phenolic concentration was determined by colorimetry using the Folin-Ciocalteu reagent and aqueous sodium carbonate. Although this method may extract a variety of phenolics, consistent negative relations with N mineralization have been found (Palm and Rowland 1997). It may therefore give a crude but meaningful overall indication of the effects of bulk soluble phenolics on decomposition and plant growth conditions. Initial lignin concentration was determined as described in Poorter and Villar (1997). In brief, after ground, oven-dry plant material has undergone several (polar, non-polar and acid) extraction steps, the mass of the residue, corrected for ash content, and its C and N concentrations are used to calculate the lignin concentration based on the difference in C content between cellulose and lignin, after correction for remaining proteins. Although the so-called 'lignin' fraction determined in this and frequently applied other methods (acid-insoluble carbon, Klason lignin) may contain other recalcitrant C-fractions besides true lignin, it has often successfully been used as a litter quality index (Hobbie 1996, Preston et al. 1997 and references therein). For brevity, we will further refer to this fraction as lignin. Average decomposition per litter species and their initial chemistry values are given in the appendix.

Data analyses

The effects of inorganic fertilizer on phytometer biomass were analyzed by one-way ANCOVA models, and litter amount and litter species effects (litter quantity experiment) on biomass by two-way ANCOVA models. Growth form effects on biomass were analyzed by nested

ANCOVA models, with species nested within growth form. For all ANCOVA models we used initial total leaf length as the covariate, as the best measure for initial biomass. Although initial total leaf length accounted for only part of the variation in initial biomass, the relation was highly significant ($R^2 = 0.38$, $P = 0.001$), and it was a significant covariate in most of the ANCOVA models. Growth form effects on biomass increase in the second year (biomass after 21.5 months minus biomass after 9.5 months) were analyzed by nested two-way ANOVA models, with species nested within growth form. All tests were followed by Tukey HSD post-hoc tests in cases where one or more fixed factors were significant. To examine the overall effects of the leaf litters in the growth form experiment on the phytometers, we calculated response ratios (ln[treatment response/control response]) of biomass after 9.5 or 21.5 months or biomass increase in the second year for each litter species, and tested for their overall deviation from zero (t-test). Furthermore, we compared the biomass of each separate litter species with that of the control treatment (Dunnett t-tests). To investigate the relation between phytometer biomass or production, and litter decomposability (expressed as litter mass loss after 21.5 months) or litter chemistry (initial N, P, C, phenol and lignin concentrations, C/N, C/P, phenol/N, phenol/P, lignin/N and lignin/P ratios), we used simple linear regression analyses, with averaged values for each litter species in the growth form experiment.

Homogeneity of variances was tested with Levene's test. Data were ln-transformed if needed to improve the homogeneity of variances (initial P and phenol concentrations, initial C/N, C/P, phenol/N and phenol/P ratios). Litter mass loss fractions were arcsine-square-root transformed. All statistical analyses were performed with SPSS for Windows 10.1.

RESULTS

Effects of inorganic nutrients

The phytometer plants in our experiment were clearly nutrient-limited and showed strong biomass responses to the addition of inorganic N and P (Fig. 1; one-way ANCOVAS: 9.5 months: initial total leaf length: $F = 4.2$, $P = 0.054$, nutrient level: $F = 72.5$, $P < 0.001$; 21.5 months: initial total leaf length: $F = 4.3$, $P = 0.051$, nutrient level: $F = 205.2$, $P < 0.001$). The addition of the inorganic form of only 25 – 50 % of the total initial N and P content in the most nutrient-rich leaf litter in our experiment increased the phytometer biomass by 37-104% after 9.5 months, and by 80-190% after 21.5 months.

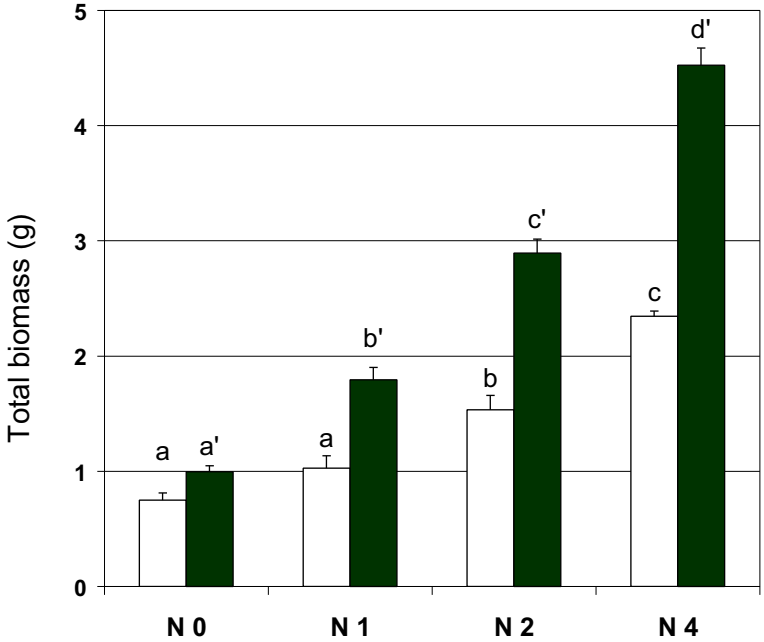

Fig. 1 Total biomass (mean + SE) of four *Poa alpina* phytometers per pot, after 9.5 (white bars) and 21.5 months (black bars), and fertilization with inorganic nitrogen and phosphate (n = 6). Different letters indicate significant differences between nutrient levels within each harvest ($P < 0.005$, Tukey HSD). Nutrient additions (pot^{-1} $season^{-1}$): N0 (control): 0 mg N, 0 mg P; N1: 7.5 mg N, 1.1 mg P; N2: 15 mg N, 2.3 mg P; N4: 30 mg N, 4.5 mg P.

Effects of leaf litter quantity

Phytometer biomass at both harvests did not show a significant general response to the increasing litter amounts (Table 2, Fig. 2). There was a trend ($P < 0.10$) for a somewhat lower biomass after 9.5 months in pots with *P. palustris* litter than in those with *C. rostrata* litter. Biomass after 21.5 months differed significantly among the treatments with the three different litter species (Table 2), with an average reduction in biomass of 21 and 14 % for the *E. nigrum* and *P. palustris* litter treatments, respectively, compared with the *C. rostrata* treatment. However, this species effect interacted with litter quantity (Table 2). Further analyses of the data for each species individually showed that litter quantity only had a significantly negative effect in case of *E. nigrum* litter (Fig. 2, one-way ANCOVA, initial leaf length: $F = 28.34$, $P < 0.001$, litter amount: $F = 10.30$, $P = 0.002$), of which 2 and 3 g reduced the phytometer biomass by 10 and 22 %, respectively, compared with 1 g litter.

Overall, growth form, and species related effects

Overall, total biomass after 9.5 months was lower (up to 49 %) for phytometers treated with leaf litters than for untreated plants (average response ratio = -0.29, $t = -9.1$, $P < 0.001$) (Fig. 3). However, the phytometers responded distinctly to leaf litters of individual species.

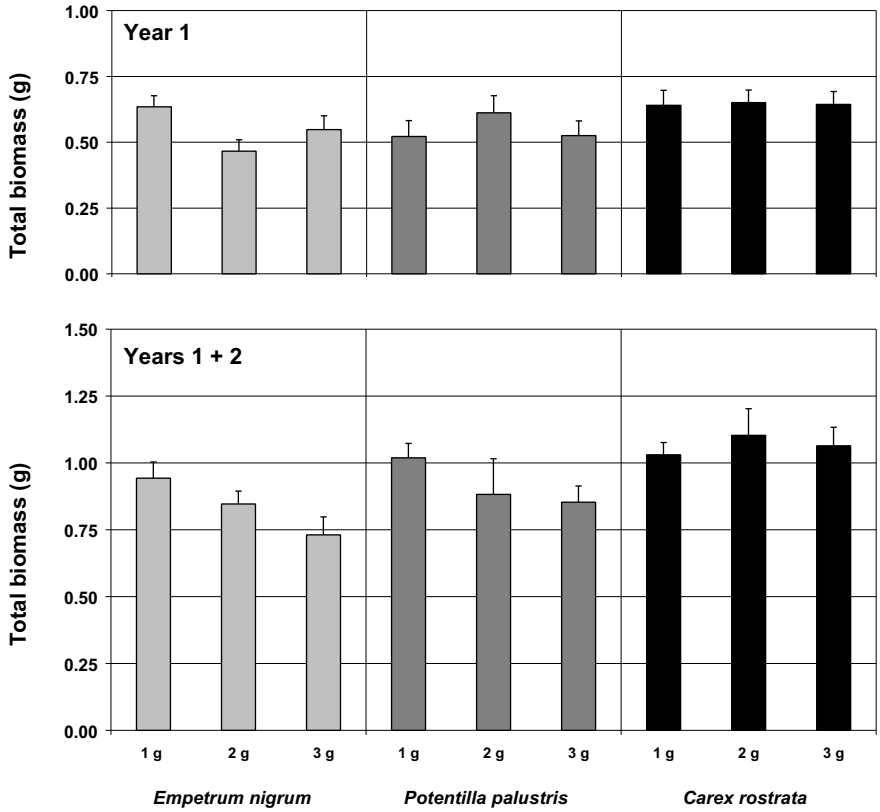

Fig. 2 Total biomass (mean + SE; n = 6) after 9.5 (upper graph) and 21.5 months (lower graph) of four *Poa alpina* phytometers per pot, growing with 1, 2 or 3 g leaf litter of one of three different species on top of the soil.

Table 2 Results of ANCOVA models of biomass response of *Poa alpina*, grown for 9.5 and 21.5 months with three different amounts of leaf litter of three contrasting species (n = 6, but n = 3 for *Empetrum nigrum* (2 g) and *Potentilla palustris* (2 g) after 9.5 months). Initial total leaf length was included in the models as a covariate.

Variable	Source	F	P
Biomass 9.5 months	Initial total leaf length	1.05	0.31
	Litter amount	0.20	0.82
	Species	3.03	0.060
	Litter amount × species	0.82	0.52
Biomass 21.5 months	Initial total leaf length	77.09	< 0.001
	Litter amount	2.27	0.12
	Species	22.52	< 0.001
	Litter amount × species	2.90	0.033

Table 3 Results of ANCOVA and ANOVA models of biomass response after 9.5 and 21.5 months, and biomass increase in the second year of *Poa alpina*, grown with leaf litters of species of four growth forms (GF; n = 6; 5 species per growth form). Species was nested within growth form as random factor. Initial total leaf length was included in the ANCOVA models as a covariate.

Variable	Source	F	P
Biomass 9.5 months	Initial total leaf length	5.44	0.022
	GF	2.41	0.11
	Species within GF	3.95	< 0.001
Biomass increase second year	GF	2.57	0.09
	Species within GF	1.85	0.035
Biomass 21.5 months	Initial total leaf length	4.01	0.048
	GF	1.23	0.33
	Species within GF	3.39	< 0.001

Particularly the addition of several deciduous shrub and forb litters (e.g. *Arctostaphylos alpinus*, *Salix myrsinites*, *Bartsia alpina*) strongly reduced the phytometer biomass compared with most evergreen shrub and graminoid litters, but also compared with less detrimental litters of their own growth forms (e.g. *Salix lapponum*, *Betula nana*, *Bistorta vivipara*). Altogether, there were no significant differences among growth forms in litter effects on phytometer biomass, but highly significant differences among individual species (Table 3, Fig. 3).

In contrast to the first treatment period, the phytometers treated with leaf litters increased their biomass as much as or more than untreated plants in the second year (Fig. 3; average response ratio = 0.23, t = 5.2, P < 0.001). There was a trend (P < 0.10) for a stronger increase in biomass in the second year in the order evergreen shrubs < graminoids and deciduous shrubs < forbs, in addition to the significant differences among individual species (Table 3, Fig. 3). Two of the forb species in particular (*S. alpina* and *B. vivipara*) had strong, positive effects on plant growth in the second year. Differences among species were larger than in the first period. For example, plants grown with *A. alpinus* litter produced 55 % less biomass than those grown with *Saussurea alpina* litter.

Owing to the opposing effects of leaf litters in both treatment periods, phytometer biomass did not differ between the control and most of the litter treatments after 21.5 months (average response ratio = -0.05, t = -1.7, P = 0.11). There were, however, large differences among several of the litter species, which were not significantly related to the growth forms (Table 3, Fig. 3).

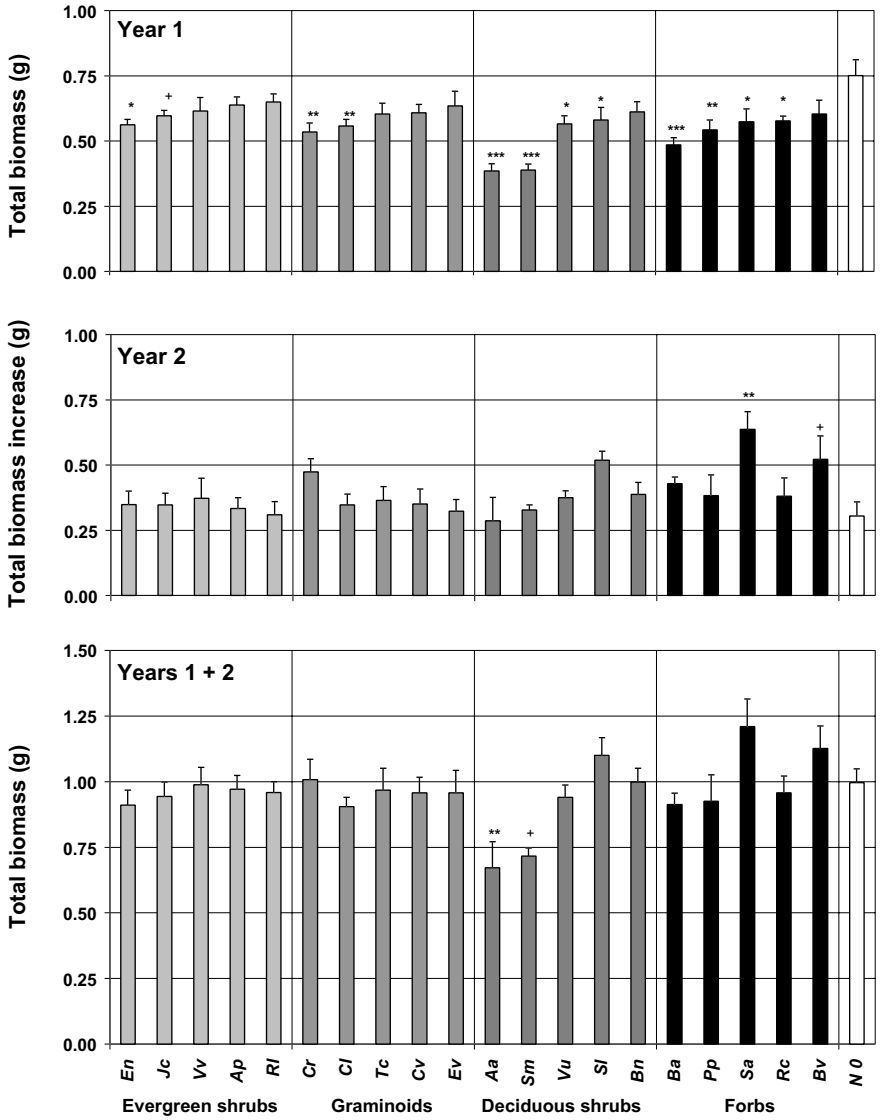

Fig. 3 Estimated total biomass (mean + SE) after 9.5 months (upper graph), total biomass increase in the second year (middle graph), and total biomass after 21.5 months (lower graph) of four *Poa alpina* phytometers per pot, growing with 2 g leaf litters of different species of four growth forms on top of the soil, or without litter (N0). For species codes, see Table 1. Bars with asterisks differ significantly from the N0 treatment within the same graph (Dunnett t-test; + $P < 0.1$;* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; $n = 6$).

Effects of leaf litter quality

Phytometer biomass after 9.5 months was negatively related to litter decomposability, and positively to initial lignin/P ratio of the litters (Table 4). It also tended to be weakly and negatively related to the initial litter phenol concentration and phenol/N ratio ($P < 0.10$).

In contrast to the biomass at the first harvest, second-year biomass increase was strongly related to several chemical variables (initial N concentration (positive), C/N, phenol/P and phenol/N ratios and C concentration (negative)), but not to the decomposability of the litter (Table 4). Second-year biomass increase showed trends ($P < 0.10$) for much weaker negative relations with initial litter phenol concentration and C/P ratio. After 21.5 months, total biomass was also not significantly related to litter mass loss, but showed strong, negative relations with initial litter phenol/N and phenol/P ratios and phenol concentration. There were weaker relations with initial litter N concentration (positive) and C/N ratio (negative).

Table 4 Model R^2 and significance level of linear regressions of *Poa alpina* biomass after 9.5 and 21.5 months, and biomass increase in the second year, on leaf litter mass loss (determined after 21.5 months) and on initial litter chemistry variables (N, P, C, phenol and lignin concentrations, and C/N, C/P, phenol/N, phenol/P, lignin/N and lignin/P ratios)

Response variable	Independent variable	R^2	P
Biomass 9.5 months	Litter mass loss	0.30	0.013
	Lignin/P	0.21 (+)	0.043
	Phenol	0.18	0.07
	Phenol/N	0.15	0.09
Biomass increase second year	Litter mass loss	0.13 (+)	0.13
	C/N	0.54	< 0.001
	N	0.53 (+)	< 0.001
	Phenol/P	0.46	0.001
	Phenol/N	0.42	0.002
	C	0.25	0.026
	Phenol	0.18	0.07
	C/P	0.15	0.09
Biomass 21.5 months	Litter mass loss	0.01	0.75
	Phenol/N	0.51	< 0.001
	Phenol/P	0.45	0.001
	Phenol	0.32	0.010
	N	0.26 (+)	0.022
	C/N	0.23	0.034

Chemistry variables with a significance level > 0.1 have been omitted from the table. Relations are negative unless otherwise (+) indicated.

DISCUSSION

Our broad screening of sub-arctic, vascular peatland species and growth forms has demonstrated that their leaf litters can exert strong effects on plant growth, which are related to the litter quality (chemistry, species identity, growth form), litter quantity, and time period. To our knowledge, this is the first experimental study that has used a large set of species of various growth forms to elucidate the general relationship between plant litter and growth conditions, and that has compared the initial and medium-term effects on mature plants. Our results indicate that those effects change dramatically over time. First-year effects of the full range of leaf litters of all growth forms were negative. In the second year, however, growth was not affected or stimulated by the litters compared with the control treatment, and the effects tended to vary among growth forms. Second-year biomass increase could not be predicted from plant biomass after 9.5 months ($R^2 = 0.01$), which indicates that the sequence of effects varied among the litters. It is therefore likely that different mechanisms have affected plant growth simultaneously.

Initial and medium-term effects of litter quality on plant production

The effects of the leaf litters on plant growth in the first year were most strongly related to litter decomposability, but, in contrast to our hypothesis (1), the relation was negative. There are several mechanisms by which high litter mass loss rates may initially be detrimental to the growth of plants. Firstly, a high decomposition rate may reflect a high microbial activity, as a result of which leaf litters may initially immobilize N. The total amount of immobilized N is positively related to the litter decomposition rate, and may be as much as 55% of the original content (Berg and Staaf 1981, Melillo et al. 1982, Hobbie 1996, Aerts and De Caluwe 1997). Negative initial litter effects on plant growth have been related to microbial immobilization of nutrients before (De Jong and Klinkhamer 1985, Van Vuuren 1992). However, microbial N immobilization in decomposing litters is not only related to decomposition rate, but also to litter nutrient status, such as the C/N ratio (Aerts and de Caluwe 1997). Our phytometers showed only weak and non-significant relations between biomass after 9.5 months and most litter chemistry variables, which suggests that microbial immobilization within the litters may explain the negative effects of part, but not all of the litters.

Secondly, for several species the negative effect of a high litter mass loss on plant growth may also have been the result of the release of labile carbohydrates or phenolic compounds. Both groups of chemicals may act as C-sources for soil microbes, thereby stimulating microbial activity and nutrient immobilization in the soil, which may explain negative effects of plant tissue extracts on growth (Horner et al. 1988, Michelsen et al. 1995, Michelsen et al. 1999). Polyphenol release may also lead to chemical immobilization

by forming persistent, insoluble complexes with N, and directly exert toxic effects on microbial decomposers and on plant roots (Swift et al. 1979, Horner et al. 1988, Kuiters 1990, Northup et al. 1995, Hättenschwiler and Vitousek 2000). The negative, albeit non-significant, relations between phenol concentration or phenol/N ratio and first-year plant growth suggest that those phenol effects may explain the negative effects of several phenol-rich litters, which is in agreement with other studies (Sydes and Grime 1981, Kuiters 1990).

The effects of litter quality on plant production was quite different in the second year of the experiment. The similar or even higher biomass increases of the phytometers growing with litter compared to those of the untreated control plants showed a strong, positive relation with initial litter N concentration and negative relations with litter C/N, phenol/N and phenol/P ratios, which is in accordance with our hypothesis (1). These results indicate that plant-available nutrients were released from nutrient-rich, but phenol-poor litters during the second year. However, contrary to our expectations differences in second-year plant growth were not related to total litter mass loss. A high decomposition rate as a result of microbial activity may thus have resulted in nutrient mineralization for some litter species in the second year, while for other litters negative phytotoxic or immobilizing effects related to a high release of phenolic compounds seem to have persisted.

Differences among growth forms in litter effects on plant production

The four major vascular peatland growth forms did not differ significantly in their negative effects on plant biomass after 9.5 months, but showed a trend for an increasingly positive effect of leaf litters on second-year plant production in the hypothesized (2) order: evergreen shrubs < graminoids or deciduous shrubs < forbs. The relation between litter decomposition, initial litter chemistry and plant growth discussed above may directly explain those results. The growth forms did not differ in litter mass loss after 21.5 months, (appendix; analyses not shown), which is in accordance with previous comparisons of several of these vascular growth forms in peatlands and other (sub)arctic ecosystems (Aerts et al. 1999, Quested et al. 2003a, Hobbie and Gough 2004, Dorrepaal et al. in press). The differences in decomposition among these four growth forms in nutrient-poor northern ecosystems are therefore probably too small to result in differences in first-year litter effects on plant growth. Significant differences in litter decomposability have been reported, however, for studies comprising of litters from a range of more and less productive ecosystems, or including a wider range of growth forms (Cornelissen 1996, Pérez-Harguindeguy et al. 2000, Quested et al. 2003a). This suggests that growth forms might be useful in predicting first-year litter effects on plant production at a larger integration level than we used, and across ecosystems varying greatly in nutrient availability.

In contrast to litter decomposition, the growth forms clearly differed in litter chemistry (appendix), which corresponds to previous reports for various ecosystems and climates (Aerts et al. 1999, Pérez-Harguindeguy et al. 2000, Shaw and Harte 2001, Dorrepaal et al. in press). Our data showed a transition from a decomposability-based relation towards a nutrient-based relation between leaf litters and plant growth in the second year. If the second-year responses were sustained beyond our experimental period, our results therefore suggest that the major vascular peatland growth forms may indeed differ in their long-term effects on plant production.

Effects of litter quantity on plant production

The comparison of litter quantity and litter quality effects on plant growth again highlighted the negative relation to fast decomposition in the first year (*P. palustris*; appendix) and a positive relation to high initial nutrient concentrations in a later phase (*C. rostrata*). However, three-fold increases in litter amount had relatively few effects and only enhanced the negative effects for phenol-rich, but nutrient-poor litter (*E. nigrum*) after 21.5 months. *E. nigrum* is known as an allelopathic species, whose leaves and leaf extracts have negative effects on germination and growth because of specific phenolic compounds (Wardle et al. 1998). However, its litter effects on plant biomass did not differ substantially from many other litters at an intermediate quantity (Fig. 3, Quested et al. 2003b), which suggests that the increasingly negative effects at higher quantities may be more widespread among phenol-rich litters. The results of *C. rostrata* and *P. palustris* litters, on the other hand, suggest that litter quantity may have little effect on total nutrient release from nutrient-rich litters, but that higher nutrient levels may ameliorate the negative medium-term effects of greater amounts of phenol-rich litter.

The 10-20% reduction in plant biomass after 21.5 months in response to 200 or 300 g m^{-2} *E. nigrum* litter compared with the 100 g m^{-2} treatment was in the same range as the average 14-21% reduction in biomass in response to *P. palustris* and *E. nigrum* litter compared with the *C. rostrata* treatments. The litter quantity effect of *E. nigrum* was in the same direction, but somewhat smaller than previously reported litter quantity effects (Sydes and Grime 1981, De Jong and Klinkhamer 1985, Foster and Gross 1997), probably because we minimized physical litter effects on light, temperature and moisture by using smaller amounts of litter and by watering the plants every day. Direct comparisons between litter quantity and litter quality effects have rarely been reported before, but the range of reported reductions in biomass in response to doubled litter amounts (10-66%) is slightly smaller than the range of effect sizes among different species (29-78%) (Schlatterer and Tisdale 1969, Ahlgren and Ahlgren 1981, Sydes and Grime 1981, De Jong and Klinkhamer 1985, Quested et al. 2003b, Fig. 3). For litter amounts up to 300 g m^{-2}, litter quality and

species identity thus seem to be at least as important as litter quantity in determining growth conditions during the first two years, which confirms our hypothesis (3).

The role of leaf litter in peatland ecosystems

Our results clearly demonstrate that even within nutrient-constrained northern peatlands, several plant species differ considerably in their positive and negative leaf litter effects on plant growth, both in the short and medium-term. The aim to unravel the temporal changes in the relation of litter chemistry and decomposability with plant growth for a broad range of species of various growth forms constrained us to a pot-experiment with one general test-plant, lasting for two growing seasons. However, the difference in effect size among species increased with time and became more strongly related to differences in initial chemistry, which makes it likely that these peatland species may also vary in their longer-term litter effects on plant growth. Differences in the composition of undisturbed plant communities or species shifts induced by external disturbances, such as climate change, may thus feed back strongly to the growth conditions and nutrient cycling rates in northern peatlands. Peatlands differing in dominant growth form have been reported to differ in nutrient mineralization rates (Aerts et al. 1999). Combined with the trend towards differential litter effects among growth forms on plant growth reported here, this suggests that growth forms might be useful in predicting medium- to longer-term litter-mediated effects of plant community changes on plant growth. The strength of the growth-form effect may, however, depend on the scale of the study and the variation in nutrient availability.

It has been postulated that plant species reinforce differences in nutrient availability among ecosystems through litter feedback effects (Wedin and Tilman 1990, Hobbie 1992, Aerts 1995, Northup et al. 1995, Cornelissen et al. 2001). Litter effects on plant growth indeed seem to vary among grassland, old field and forest ecosystems (Xiong and Nilsson 1999). Despite large differences among some species, the full range of peatland litters of contrasting growth forms included in our study exerted strong negative effects on plant growth in the first season, and even after two seasons most litters had not yet enhanced total plant biomass. Litter N concentrations are generally lower in peatlands compared to other ecosystems (Aerts et al. 1999), while concentrations of phenolic compounds are higher under climatically or nutrient-constrained conditions (Davies et al. 1964, McKey et al. 1978, Aerts and Chapin 2000, Graglia et al. 2001, Dorrepaal et al. in press). Although initial and medium-term litter effects on plant growth have not been investigated in other ecosystems for the wide range and large number of species and growth forms we used, comparisons with other studies suggest that immobilization and phytotoxic effects might indeed be more predominant and longer lasting among litters of northern peatlands (Heady 1956, Schlatterer and Tisdale 1969, Quested et al. 2003b). Our results emphasize again the

strong nutrient limitations over plant growth in peatlands, and thus the potential importance of growth strategies with a reduced dependence on mineralized nutrients, either through strong nutrient conservation (woodiness, evergreenness) or by accessing alternative nutrient sources (N-fixing, carnivory, hemiparasitism, organic N uptake via symbiosis with ericoid or ectomycorrhizas) (Read 1991, Aerts 1995, Chapin 1995, Northup et al. 1995, Aerts et al. 1999, Cornelissen et al. 2001). A further step would therefore not only be to compare the patterns found here with those in other ecosystems, but also to test whether those response patterns differ among test-plants with different growth strategies and how this would affect interspecific competition.

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Appendix Initial litter chemistry (total N, P, C, phenol and lignin concentrations) and mean litter mass loss and SEM after 9.5 (litter quantity experiment only) and 21.5 months for all species screened for litter effects on plant growth

Growth form	Species	N (mg/g)	P (mg/g)	C (mg/g)	Phenolics (mg/g)	Lignin (mg/g)	Mass loss after 9.5 months (%)	SEM	Mass loss after 21.5 months (%)	SEM
Litter quantity experiment										
Evergreen shrub	*Empetrum nigrum* 1 gram	5.5	0.32	556	63	421	29.4	0.3	43.0	0.7
	Empetrum nigrum 2 gram	5.5	0.32	556	63	421	24.7	1.0	39.1	1.2
	Empetrum nigrum 3 gram	5.5	0.32	556	63	421	20.5	0.6	36.6	1.9
Forb	*Potentilla palustris* 1 gram	9.6	0.51	471	107	120	38.6	1.9	51.4	5.8
	Potentilla palustris 2 gram	9.6	0.51	471	107	120	33.6	1.0	57.0	5.0
	Potentilla palustris 3 gram	9.6	0.51	471	107	120	32.8	0.7	52.7	2.4
Graminoid	*Carex rostrata* 1 gram	10.8	0.67	450	12	50	25.7	0.9	48.2	1.4
	Carex rostrata 2 gram	10.8	0.67	450	12	50	26.7	1.2	48.7	1.2
	Carex rostrata 3 gram	10.8	0.67	450	12	50	27.6	0.8	48.3	0.3
Growth form experiment										
Evergreen shrubs	average	7.3	0.34	531	56	360			26.0	
	Empetrum nigrum	5.5	0.32	556	63	421			39.2	1.0
	Juniperus communis	8.8	0.48	523	40	302			40.7	1.0
	Vaccinium vitis-idaea	7.1	0.34	516	53	350			17.1	0.2
	Andromeda polifolia	6.4	0.34	529	47	370			9.0	0.7
	Rhododendron lapponicum	8.5	0.21	533	77	356			23.9	1.2
Graminoids	average	6.5	0.19	452	15	61			37.1	
	Carex rotundata	8.0	0.28	445	18	37			40.3	2.1
	Calamagrostis lapponica	5.5	0.19	433	10	nd			39.6	1.4
	Trichophorum cespitosum	5.9	0.08	462	15	83			43.0	0.9
	Carex vaginata	8.2	0.27	446	20	33			42.0	1.1
	Eriophorum vaginatum	4.8	0.12	472	13	153			20.8	0.8
Deciduous shrubs	average	9.1	0.44	493	129	222			36.8	
	Arctostaphylos alpinus	6.4	0.38	499	302	161			53.5	3.4
	Salix myrsinites	8.6	0.31	480	86	158			40.7	2.2
	Vaccinium uliginosum	8.6	0.24	495	119	223			35.4	1.8
	Salix lapponum	11.5	0.74	484	49	289			27.2	0.9
	Betula nana	10.6	0.52	505	90	278			27.3	1.2
Forbs	average	12.7	0.54	456	59	135			51.5	
	Bartsia alpina	13.1	0.83	434	43	57			74.8	5.3
	Potentilla palustris	9.6	0.51	471	107	120			51.6	4.9
	Saussurea alpina	14.4	0.35	423	12	82			74.8	2.5
	Rubus chamaemorus	13.2	0.63	481	119	118			30.5	1.1
	Bistorta vivipara	13.4	0.37	472	16	302			26.0	1.4

nd = not detectable.

CHAPTER 6

GENERAL DISCUSSION

ARE PLANT GROWTH-FORM BASED CLASSIFICATIONS USEFUL IN PREDICTING ECOSYSTEM FEEDBACKS TO CLIMATE CHANGE?

Northern peatlands play an important role in the atmospheric carbon balance of our planet, and changes in their carbon uptake and release, in response to climate change, may feed back to the climate at a global scale (Gorham 1991, Houghton et al. 2001). Plant species strongly control this feedback, because differences in physiology, morphology, and physical and chemical properties of their living and dead tissues interact with almost all processes of carbon and nutrient cycling (chapter 1). In this thesis, I investigated several potential direct and plant-mediated effects of climate change on production and decomposition processes in northern peatlands, and focussed on general differences among plant species belonging to different growth forms. Plant growth forms are part of a hierarchical, functional species classification, which identifies several intermediate aggregation levels between 'individual species' and 'total vegetation' (chapter 1, Fig. 2; Chapin et al. 1996, Epstein et al. 2001).

Plant growth-form based classifications have become a widely used tool in arctic ecology to investigate and generalise the responses of plants to their environment, as well as their effects on ecosystem processes (e.g. Chapin et al. 1995, Jonasson et al. 1999, Arft et al. 1999, Aerts & Chapin 2000, Quested et al. 2003a). Their responses and effects are expected to differ, based upon ecological field experience, theoretical considerations, and cluster analysis (Chapin et al. 1996). Moreover, their easy identification and circumpolar distribution greatly facilitate large-scale comparisons among studies and sites (Arft et al. 1999, Cornelissen et al. 2001, Dormann & Woodin 2002, Van Wijk et al. 2003).

A hierarchical classification may distinguish a large number of supposedly different groups (chapter 1, Fig. 2; see Chapin et al. 1996 for more sub-divisions). However, high levels of detail may be unpractical, and not even useful. If two or more groups co-vary in their responses and effects, it would be inefficient to treat them as separate groups. On the other hand, if the species within groups appear to differ as much as species of different groups, that particular level of separation or aggregation would not be very useful either (Epstein et al. 2001). It is therefore important to determine which sub-divisions, and how many groups, are actually useful. The minimum number of useful functional groups, needed to describe and predict the role of plants in ecosystem functioning, may depend on the response or effect considered. In relation to the feedback of northern peatlands to climate change, we should consider growth and production responses, as well as plant effects on decomposition and nutrient availability (Shaver et al. 2000, chapter 1). Useful sub-divisions should then separate hierarchical groups of the growth-form based classification that comply with the following conditions:

(1) Groups should differ on average from each other in their response or effect size under identical conditions.
(2) Groups should represent less variation therein among the species within groups than among species of different groups.
(3) Groups should differ consistently from each other under changing conditions.

So far, several of these conditions have been investigated for different sets of growth forms, and for various of their responses to environmental disturbances or effects on ecosystem processes. In this chapter, I will discuss the usefulness and limitations of the growth-form concept in predicting climate change effects on production and decomposition, based on the data presented in this thesis as well as in other studies, and I will indicate aspects on which we need additional information.

PLANT GROWTH-FORM AND CLIMATE CONTROLS ON PRODUCTION IN NORTHERN PEATLANDS

During the past decades, much effort has been made to investigate whether plant species and growth forms differ in their growth and biomass production responses to climate change and associated increases in nutrient availability. This would allow us to make accurate predictions of future carbon sequestration for a range of ecosystems, based on their current community composition. Furthermore, it would facilitate predictions of the future community composition, and thus the quality and quantity of the litter input into the decomposition and mineralisation sub-system of these ecosystems. Indeed, in many whole-ecosystem manipulations of environmental factors, changes in biomass, productivity, or plant cover appeared to differ among one or several species of different growth forms (e.g. Chapin & Shaver 1985, Press et al. 1998, Robinson et al. 1998, Graglia et al. 2001). In the chapters 2 and 3 of this thesis, we have for example shown that increased winter snow cover may strongly enhance the biomass production of the peat-moss *Sphagnum fuscum*, but does not seem to affect four common sub-arctic vascular plant species (*Betula nana*, *Empetrum nigrum*, *Calamagrostis lapponica*, and *Rubus chamaemorus*).

Individual studies of species responses to environmental manipulation may indicate possible differences among groups of species. Moreover, if the investigated species represent the majority of biomass or production, the results may indicate the overall responses at the growth-form level for a particular ecosystem. However, are these responses representative for the respective growth forms, or are they in fact species-specific? So far, a comprehensive analysis of the three above-mentioned conditions in arctic ecosystems has been complicated by the usually limited number of species per growth form present in a single ecosystem, and the varying initial conditions and treatments applied across the experimental sites. If we confine ourselves to summer warming studies and fertilisation studies, several general conclusions can nevertheless be drawn, using two different, common approaches.

One approach has been to analyse whether the responses of individual species within growth forms are similar, but differ from those of other growth forms (conditions 1 and 2). Chapin et al. (1995) compared two or three species per growth form in tussock tundra in Alaska, and concluded that the species were generally similar in their responses to nutrients, but not to temperature. They further suggested that enhanced nutrient availability would initially increase the abundance of graminoids, followed by deciduous shrubs, and reduce the abundance of evergreen shrubs, mosses and lichens. Hobbie & Chapin (1998) and Hobbie et al. (1999) reported a similar inconsistency in the temperature responses of a wider range of vascular plant species in the Alaskan tussock tundra, but a general reduction in the biomass of the majority of the non-vascular plants. In a sub-arctic dwarf shrub heath, on the other hand, vascular plant species responses to nutrient addition seemed to be more

species-specific compared with their mostly positive responses to temperature (Press et al. 1998). Again, many bryophytes and lichens decreased in abundance in response to both manipulations. Across the arctic, a meta-analysis of species-level responses in 36 experiments showed generally few and small differences among the growth forms (Dormann & Woodin 2002). Warming stimulated grasses and shrubs compared with other growth forms, while nutrient addition only increased the biomass of grasses compared with all other groups. Unfortunately, the data were not further analysed with respect to different ecosystem types or regions. It therefore remained unclear whether the absence of clear differences among most of the growth forms was genuine, or caused by interactions between growth-form responses and different ecosystem types, regions or other factors (condition 3).

Another approach has been to start with aggregating all species present in an ecosystem into growth forms, and then measure the total biomass or production response of each growth form (Press et al. 1998, Shaver et al. 1998, Jonasson et al. 1999, Van Wijk et al. 2003). This integrated measure is highly sensitive to strong responses of only one or two species, as have been observed in several experiments (Press et al. 1998, Chapin et al. 1995). Whilst it may be interpreted as a weighted average response of the species in each growth form (condition 1), it does not reveal whether the species within growth forms respond homogeneously (condition 2). Furthermore, this approach requires analysis of multiple experiments in order to investigate generalities. Repeated sampling and a detailed meta-analysis of the responses of growth forms in eight experiments in heath, tussock tundra and wet sedge tundra in Alaska and north Sweden showed that the effects of nutrients or temperature on vascular plant growth forms may differ strongly among regions, ecosystem types, and duration of the experimental treatment (Chapin et al. 1995, Van Wijk et al. 2003). In contrast, a consistent pattern was again a negative correlation between the responses of non-vascular plants or lichens, and shrubs (Cornelissen et al. 2001, Van Wijk et al. 2003).

Vascular plants versus non-vascular cryptogams

The difference in response between vascular plants and non-vascular cryptogams thus appears to be general, and seems to be strongly related to the low position of mosses and lichens in the vegetation, and their relatively high sensitivity to drought. In many ecosystems, high levels of fertilisation or air warming strongly increased the aboveground biomass of vascular plants or their litter, or increased the vapour pressure deficit (VPD). Both increased shading and VPD indirectly resulted in overall negative effects on mosses and lichens (Berendse et al. 2001, Cornelissen et al. 2001, Weltzin et al. 2001, Van Wijk et al. 2003, Gunnarsson et al. 2004), although direct, damaging fertilisation effects can not be ruled out as an additional factor. This contrasts with positive, direct responses of certain

bryophyte species to nutrient addition in more open ecosystems, such as a high arctic semi-dessert (Robinson et al. 1998), frost-heaved tundra (Jonasson 1992), a sub-arctic fellfield (Jonasson et al. 1999), and a sub-arctic bog (Aerts et al. 1992b). Furthermore, realistic increases in summer temperatures do not necessarily increase the VPD (chapter 2), and under these conditions *Sphagnum* growth and possibly its biomass production may be strongly enhanced (Sonesson et al. 2002, chapter 2). In chapter 3, we have indicated that increased overgrowth by *Sphagnum*, due to and in combination with summer warming, might prevent future expansion of the aboveground vascular plant canopy in sub-arctic peatlands. Also, thicker lichen carpets are known to suppress vascular plant regeneration in boreal forests (Helle & Aspi 1983). A negative correlation between the responses of vascular plants and non-vascular cryptogams does therefore not imply that the responses of mosses to climate change are always negative.

Altogether, it seems that plant growth forms, particularly vascular plants versus non-vascular groups, may differ in their average biomass and production responses to summer climate-change factors within single ecosystems (condition 1). However, species within growth forms do not always show similar responses under identical conditions (condition 2). Furthermore, the responses of both species and growth forms seem to be strongly dependent on the initial conditions and the exact consequences (including possible artefacts) of the treatments applied (condition 3). The causes and mechanisms of these inconsistencies remain poorly understood so far, but explaining factors may include differences in soil nutrient availability, moisture conditions, ecosystem biomass and productivity, community-dependent competitive, facilitative or trophic interactions, and the harshness of the climate, including winter snow conditions (Arft et al. 1999, Cornelissen et al. 2001, Van Wijk et al. 2003). In order to determine the usefulness of a growth-form based classification in generalising the responses of plant species to climate change, we clearly need a better understanding of these interacting factors. This requires to expand the range of investigated conditions, by including a wider range of ecosystems and regions, and by manipulating and monitoring more realistic scenarios of climate change throughout the year.

PLANT GROWTH-FORM AND CLIMATE CONTROLS ON DECOMPOSITION FEEDBACKS IN NORTHERN PEATLANDS

Decomposition and mineralisation of dead plant tissues are key processes in the long-term feedback of northern peatlands to climate change and the global carbon balance. Because of the unfavourable environmental conditions in northern peatlands, decay of organic matter is often the rate-limiting step in carbon cycling. It does not only control the size and turnover of the organic carbon pool in the soil, and thus the release of CO_2 or CH_4 into the

atmosphere. Microbial breakdown of organic matter and the mineralisation of nutrients also regulate the availability of nutrients for plant growth, and thus the long-term carbon sequestration capacity of northern peatlands.

Climate change may directly enhance decomposition and mineralisation processes, but in the longer term these effects seem to be restricted by the quality of the organic matter (Hobbie 1996, Christensen et al. 1999, Rustad et al. 2001, Shaw & Harte 2001). Climate change or associated changes in nutrient availability may, however, alter the physical or chemical quality of litter, both within species and through changes in the plant community composition (Harte & Shaw 1995, Press et al. 1998, Shaw & Harte 2001, Van Heerwaarden et al. 2003). For example, in chapter 3 we have shown that summer warming decreased the nitrogen (N) concentration in *Betula nana* leaf litter. In chapter 4 we have shown that N, phosphorus (P), and phenol concentrations of the leaf litters of five plant growth forms differed among three regions along a large-scale environmental gradient. Differences in litter chemistry among species and growth forms may, however, be much larger than differences related to variation in environmental conditions, as was indicated in chapters 3 and 4 as well. As a consequence, these interspecific differences in litter chemistry may have greater effects on decomposition than temperature directly (Hobbie 1996, Robinson et al. 1995, Shaw & Harte 2001). Longer-term, climate-change induced shifts in plant community composition may therefore be at least as important for ecosystem-level decomposition rates and nutrient availability as direct environmental effects (Berendse 1994, Hobbie 1996, Hobbie et al. 2000), and a growth-form based classification might be useful to predict these plant-mediated effects.

Growth-form and climate controls on decomposition

The usefulness of plant growth forms as predictors of community-change effects on ecosystem-level decomposition has been addressed in several studies, comprising different sub-sets of growth forms, different numbers of species per group, and various ecosystems (Cornelissen 1996, Hobbie 1996, Aerts et al. 1999, Pérez-Harguindeguy et al. 2000, Quested et al. 2003a, chapter 4). Most of these studies have indicated that some growth forms indeed differ in their average decomposition rates (condition 1). Forb litters usually decompose fastest (Cornelissen 1996, Pérez-Harguindeguy et al. 2000, Quested et al. 2003a), and *Sphagnum* or other moss litters decompose much slower (Coulson & Butterfield 1978, Hobbie 1996, Aerts et al. 1999, chapter 4) than the litters of evergreen and deciduous shrubs, and graminoids. Some studies have also indicated that species within growth forms resembled one another in decomposition rates (Hobbie 1996), or, when tested explicitly, that growth forms accounted for a significant part of the total variation in litter decomposition (Cornelissen 1996, Aerts et al. 1999, Aerts & Chapin 2000, Pérez-Harguindeguy et al.

2000, Quested et al. 2003a) (condition 2). In chapter 4, however, we have for the first time explicitly tested whether the relative differences in decomposability among growth forms of a single ecosystem are robust against changes in environmental conditions (condition 3). Our results clearly indicated that this is not the case, even though the growth forms showed large and consistent differences in litter chemistry. While the litters of some growth forms decomposed much faster under milder conditions than at higher latitudes (i.e. forbs), the decomposition of litters of other growth forms seemed relatively insensitive to changes in environmental conditions (i.e. *Sphagnum*, evergreen shrubs). Furthermore, the differences among several of the growth forms, particularly the three most abundant vascular growth forms in northern peatlands and many arctic ecosystems, i.e. evergreen shrubs, deciduous shrubs and graminoids, were relatively small and their ranking differed across the regions.

Although interactive effects of environmental conditions and species on decomposition have not been tested before for a comparably wide range of species and growth forms, our results are supported by several smaller-scale studies, which may indicate some of the mechanisms involved. Hobbie (1996) investigated the effect of increased temperatures on decomposition of seven arctic species, and concluded that the decomposition of mosses was less affected by increases in temperature than that of vascular plants. The sensitivity of the decomposition rate of two moss species to differences in soil pH and N availability between two contrasting tundra sites was also much lower than that of several vascular plant species (Hobbie & Gough 2004). The generally slow decomposition of *Sphagnum* mosses in peatlands has been attributed to both abiotic conditions (low pH, low temperature, waterlogged, anaerobic conditions), and to their low N concentration and high concentrations of various decay-resistant or decay-inhibiting compounds (Clymo & Hayward 1982, Johnson & Damman 1993, Verhoeven & Toth 1995). The fact that *Sphagnum* decomposition is usually much slower than that of vascular litters, even under identical conditions (Hobbie 1996, Scheffer et al. 2001, Hobbie & Gough 2004, chapter 4), indicates that its poor litter quality may be a much stronger constraint for decomposition than the abiotic conditions. Strong intrinsic physical and chemical constraints might thus explain the weak response of the decomposition of litters of *Sphagnum*, and possibly of some slow decomposing vascular growth forms, to increased temperatures or changes in other environmental conditions.

The relation between *Sphagnum* decomposition and the environmental conditions along the latitudinal gradient in chapter 4 may thus have differed from that of some of the other growth forms, but this did not affect the relative ranking of *Sphagnum* according to its decomposition. *Sphagnum* litters therefore seem to decompose more slowly than vascular leaf litters, irrespective of the environmental conditions, which confirms various earlier observations (Coulson & Butterfield 1978, Verhoeven & Toth 1995, Hobbie 1996, Aerts

et al. 1999, Scheffer et al. 2001). The differences in decomposability among the vascular growth forms, as well as their relative ranking, was, however, much less consistent across the regions (chapter 4), and also varied among other studies (Cornelissen 1996, Aerts et al. 1999. Aerts & Chapin 2000, Quested et al. 2003a, Hobbie & Gough 2004). This may be explained at least partly by environmental controls on the relation between their litter chemistry and decomposition. Litter decomposability has been related successfully to various litter properties, including the concentrations of lignin, N, P, carbon, phenols, and cellulose, or ratios thereof (e.g. Melillo et al. 1982, Hobbie 1996, Aerts & Chapin 2000). However, ecosystems or regions subjected to strong adverse conditions are generally characterised by weaker relations between decomposition and individual litter quality variables than milder regions (Aerts 1997, Cornelissen et al. 1999, chapter 4). Small differences in litter decomposition among evergreen and deciduous shrubs and graminoids in nutrient-poor peatlands and other high-latitude ecosystems (Aerts et al. 1999, Quested et al. 2003a, Hobbie & Gough 2004, chapter 4), despite large differences in various individual litter chemistry variables, may thus reflect a strong climatic constraint, as well as the combined, negative effects of a range of litter properties, on decomposition.

The value of a vascular plant growth-form based classification for a consistent prediction of climate-warming effects on leaf litter decomposition at high latitudes thus seems limited. However, for a proper prediction of growth-form controls on litter decomposition at an ecosystem level, we should not only consider differences in leaf litter decomposability, but also differences in allocation and decomposability of other litter types. Leaf tissue may represent 60 % of the annual production of evergreen shrubs, but only as much as 30-40 % in graminoids and deciduous shrubs (Hobbie 1996). However, because of experimental and practical limitations, stem and root litter production and particularly decomposability have received far less attention than that of leaves. Graminoids allocate much more of their biomass to roots, and deciduous shrubs to stem tissue (Aerts et al. 1992a, Hobbie 1996). Both stem and root tissues may have lower turnover rates than (non-evergreen) leaves (Berendse & Jonasson 1992, Gill & Jackson 2000), and decompose much more slowly than leaf litter (Heal et al. 1978, Hobbie 1996, Robinson et al. 1997, Scheffer & Aerts 2000). However, broad screenings of stem and root decomposition including a range of species and growth forms have not yet been performed. Because of the combined effect of differences in allocation, turnover and potentially different decomposability of the various plant tissues, whole-plant decomposition rates may differ much more strongly among vascular growth forms than leaf-level decomposition. Future research on the usefulness of vascular plant growth forms in predicting differences in litter decay in northern peatlands should therefore focus more on the consistency of differences in whole-plant litter production and decomposability.

Growth-form controls on litter feedbacks to plant production

The usefulness of a growth-form based classification in predictions of litter effects on plant growth conditions, through the release of nutrients and other plant-available compounds, has received far less attention than their differences in leaf litter decomposability. Various studies have measured changes in litter N or P contents during decomposition (e.g. Heal et al. 1978, Berg & Staaf 1981, Hobbie 1996, Aerts & De Caluwe 1997). However, the availability of the lost nutrients for plant growth may strongly depend on the timing of release (Hobbie & Chapin 1996), the nutritional status of the organic horizon, interactions with other released chemical compounds such as phenols (Northup et al. 1995, Hättenschwiler & Vitousek 2000), and the abundance and activity of micro-organisms (Jonasson et al. 1996, Kaye & Hart 1997). Other studies have therefore directly investigated the effects of litters on plant growth. Because of practical, experimental constraints most of these studies have compared only the initial (< 1 year) litter effects of a limited number of species or growth forms (e.g. Sydes & Grime 1981, Xiong & Nilsson 1999, Quested et al. 2003b). The data presented in chapter 5 of this thesis are therefore the first thorough investigation of differences among a broad set of plant growth forms in their litter effects on plant growth during the first 2 years after fresh litter enters the decomposition sub-system. The results showed that four common vascular growth forms in arctic and sub-arctic ecosystems (evergreen and deciduous shrubs, graminoids, and forbs) do not differ significantly in their first-year leaf litter effects on plant growth, which were predominantly negative. The main reason for this was that initial litter effects were most strongly related to litter decomposability, which was not clearly related to growth form identity. However, as we discussed in chapter 5, the trend towards differences in the litter effects of the growth forms on second-year plant production suggests that vascular growth forms may indeed differ in their longer-term litter effects (conditions 1 and 2).

Because of practical constraints, we could not include *Sphagnum* in the experiment presented in chapter 5. However, because of its strongly deviating litter properties, and its high abundance in northern peatlands, it is important to consider at least the potential effects of *Sphagnum* litter on plant growth. The (negative) first-year litter effects reported in chapter 5 were most strongly and negatively related to litter decomposability, while the (positive) second-year effects were even more strongly and negatively related to initial litter C/N ratio. The extremely low decomposability and relatively high C/N ratio of dead *Sphagnum* tissues (Coulson & Butterfield 1978, Johnson & Damman 1993, Verhoeven & Toth 1995, Hobbie & Gough 2004, chapter 4) thus suggest that both the initial negative effects and the longer-term positive effects of *Sphagnum* litter may be limited compared with vascular plant litters. Preliminary results of a subsequent phytometer experiment appeared to confirm this partly (Fig. 1): after one growing season, *Sphagnum* litters seemed to have a less negative effect

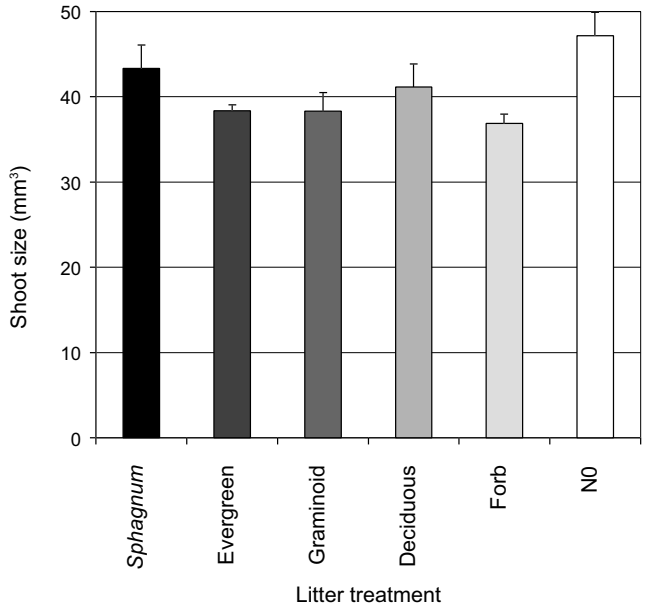

Fig. 1 Aboveground plant size (mean + SE; n = 6) of 2-year old *Betula nana* phytometers (four per pot), grown for 4 months with 2 g leaf litter of different species of five different growth forms (three species per growth form) on top of the soil, or without litter (N0) (E. Dorrepaal, unpublished results). Methods and location of plant growth, litter collection, and litter treatments were as described in chapters 4 and 5. *Betula nana* plants were grown from locally collected seeds. Plant size after the first treatment season was estimated assuming a regularly tapering cone-shape of stem and branches (cone volume = π * base radius^2 * length / 3), and adding up their estimated volumes.

on the dwarf shrub *Betula nana* than leaf litters of four vascular peatland growth forms. Strong inhibition of vascular plant growth by the excretion of high amounts of allelopathic phenolic compounds, as reported for actively growing *Sphagnum* (Verhoeven & Liefveld 1997), might thus not be an important effect of dead *Sphagnum*. In contrast, the low content of easily degradable carbohydrates and strong tanning properties of dead *Sphagnum* may inhibit microbial activity (Johnson & Damman 1993, Hobbie 1996, Verhoeven & Liefveld 1997, Scheffer et al. 2001), thereby reducing initial negative effects of microbial N immobilisation, but also reducing longer-term nutrient release. Whether or not *Sphagnum* and vascular growth forms differ substantially in their longer-term litter effects on plant growth remains to be investigated. It seems likely, however, that the relatively nutrient-rich vascular leaf litters investigated in chapter 5 are a primary, longer-term nutrient source for plant growth in *Sphagnum*-dominated peatlands.

A comparison of our results with experiments under different environmental conditions, to determine the consistency of the patterns, is unfortunately not possible yet. However, the second-year effects of the leaf litters were well related to various initial litter chemistry variables. In contrast to litter decomposability, the rankings of growth forms

according to differences in a range of litter chemistry variables were generally consistent across the large-scale environmental gradient in chapter 4. This strongly suggests that growth forms may also be consistent predictors of longer-term leaf-litter effects on plant growth (condition 3).

CONCLUSIONS

Plant species of different growth forms may differ substantially in their growth and production responses to climate change, and in their effects on decomposition and mineralisation processes. However, not all sub-divisions of the growth-form based classification may be necessary or useful to generalise individual responses or effects. To distinguish vascular plants and (*Sphagnum*) mosses seems to be essential for all generalisations, because of their often opposite growth and production responses and direct mutual interactions, and their strongly differing decomposability. Further sub-divisions into woody versus non-woody plants may be needed to include interspecific competition and whole-plant litter production and decomposability. The most detailed sub-division discussed here, differentiating evergreen and deciduous shrubs, forbs, and graminoids, may be useful in predicting longer-term litter feedbacks to plant growth. At almost all hierarchical levels, however, the usefulness of the sub-divisions clearly depends on our understanding of how the responses and effects of the growth forms vary with local and regional biotic and abiotic conditions, and the exact changes in climate throughout the year.

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SUMMARY

PLANT GROWTH-FORM AND CLIMATE CONTROLS ON PRODUCTION AND DECOMPOSITION IN NORTHERN PEATLANDS

Northern peatlands cover large areas in arctic, sub-arctic and boreal regions, and play an important role in the carbon balance of our planet. For a long time, northern peatlands have acted as net carbon sinks, because of a slower release of carbon through the decomposition of dead, organic tissues than sequestration of atmospheric CO_2 through the production of new plant biomass. The cycling of carbon in peatlands is tightly linked to the cycles of other nutrients, such as nitrogen (N) and phosphorus (P), through plant production and decomposition. Both processes are controlled by characteristics of the plants that compose the vegetation, which is usually dominated by peat mosses (*Sphagnum* spp.), and by various unfavourable environmental conditions, including low temperatures throughout large parts of the year, anoxia and low nutrient inputs.

Pronounced changes in summer and winter climate, including increases in temperature and changes in precipitation, are expected to take place at northern high latitudes during the next 50-100 years. These changes may directly alter biomass production and

decomposition rates, but also result in indirect changes by altering the species composition of the vegetation. Plant-mediated impacts may be particularly important in the longer term. However, because of the substantial differences in species composition of northern peatlands, a functional classification of plant species is needed in order to generalise their responses to climate change and their effects on ecosystem processes. This thesis aims to investigate how climate change will alter key components of the carbon cycle of northern peatlands through changes in plant production and decomposition, and particularly whether the indirect, plant-mediated effects of climate change can be generalised by grouping different plant species according to their growth forms (i.e. *Sphagnum* mosses, evergreen shrubs, deciduous shrubs, graminoids, and forbs).

The first part of this thesis focussed on the effects of changes in summer and winter climate on the growth and production of typical peatland species belonging to different plant growth forms. We experimentally manipulated the temperatures and snow conditions in a sub-arctic blanket bog using open-top chambers (OTCs), and created six climate regimes, mimicking possible future scenarios, including independent changes during summer, winter, and spring. In **chapter 2** we reported the effects of the treatments on the microclimate. The OTCs doubled the snow thickness in winter, resulting in 0.5-2.8 °C higher average air temperatures. Spring air temperatures in OTCs increased by 1.0 °C. Summer warming had a maximum effect of 0.9 °C, while vapour pressure deficit was not affected.

In the same chapter we continued by investigating the responses of summer length growth, carpet structure and production of the dominant peat-forming moss *Sphagnum fuscum* to the experimentally induced changes in climate. The small, but realistic climate manipulations had strong effects on *S. fuscum*. Summer warming enhanced the length increment by 42-62 %, whereas bulk density decreased. This resulted in a trend ($P < 0.10$) of enhanced biomass production. The winter snow addition treatments enhanced biomass production by 33 %, despite the fact that length growth and bulk density did not change significantly. The addition of spring warming to snow addition alone did not significantly enhance the snow effect, but our measurements may have missed part of the early spring growth. There were no interactions between the manipulations in summer and those in winter/spring, which indicated that the effects were additive.

The results of **chapter 2** indicated that increased winter snow thickness may increase the carbon balance of northern peatlands, because it enhanced the production of *S. fuscum* without affecting its structure. Warmer summers may, however, in the long term negatively affect the biomass productivity of the peat mosses, through the adverse effects of changes in *Sphagnum* structure on moisture retention and transport capacity. Moreover, the

strong increase in length growth of *Sphagnum* might affect interactions with other mosses and vascular plants.

The possible role of *Sphagnum* as a modifier of climate change effects on vascular plants was followed up in **chapter 3**. Because vascular plant growth forms differ in their strategies to cope with the harsh climate and low nutrient availability in northern peatlands, as well as with the progressively increasing height of the *Sphagnum* carpet in which they grow, climate change may differentially affect them. These effects may act directly and through changes in the length growth of *Sphagnum* mosses. We therefore investigated both the direct and *Sphagnum*-mediated effects of the experimental changes in summer, winter and spring climate on four species representing contrasting vascular growth forms (evergreen and deciduous shrubs, graminoid, forb), by studying their biomass- and nitrogen losses through leaf litter production, and the length growth of the two shrubs.

The direct and indirect effects of summer warming differed among the growth forms. Enhanced *Sphagnum* overgrowth of leaves due to summer warming initially stimulated leaf litter losses of the evergreen shrub *Empetrum nigrum*. However, changes in its shoot morphology, related to an apparent, small increase in its length growth, probably prevented further effects. A stronger increase in stem growth of the deciduous shrub *Betula nana* in response to summer warming directly reduced its leaf litter mass, N concentration and N losses. This change in allocation prevented indirect, *Sphagnum*-mediated effects on its leaf and N dynamics through overgrowth of buds. In contrast, leaf litter mass, N concentrations or N losses of the forb *Rubus chamaemorus* and the graminoid *Calamagrostis lapponica* were not affected by summer warming or enhanced *Sphagnum* growth. Increases in winter snow cover, with or without spring warming, did not affect the growth of the shrubs, nor the total shoot leaf litter mass or N dynamics of any of the growth forms.

We concluded that summer warming is likely to enhance *Sphagnum* overgrowth of small shrubs with a limited growth response, such as *Empetrum*. Moreover, increased vertical growth may allow *Sphagnum* to keep pace with responsive shrubs with an inclined shoot placement, such as *Betula*. This might prevent net positive effects of summer warming on the canopy height, and negate longer-term benefits of enhanced snow cover for these taller shrubs. However, leaf litter production and related nutrient dynamics are more likely affected by direct warming effects on shoot morphology and allocation than by *Sphagnum* growth. The different responses of the growth forms to summer warming suggested that both direct and *Sphagnum*-mediated climate effects have the potential to change the vascular plant community structure and nutrient dynamics in peatlands.

In the second part of this thesis I focussed on the decomposition of dead leaves, and the question whether growth forms can be used to generalise differences among plant species.

Plant growth forms are widely used to predict the effects of environmental changes, such as climate warming and increased nitrogen deposition, on plant communities, and the consequences of species shifts for carbon and nutrient cycling. However, the robustness to environmental change of the ranking of the growth forms according to their litter chemistry or decomposability remained to be established. In **chapter 4** we therefore investigated whether a functional classification based on growth forms results in a consistent prediction of patterns in litter quality and decomposition, independent of the environmental conditions. Furthermore, we tested whether growth forms are as good at predicting decomposability as a set of the most widely used litter chemistry variables. We used a natural, latitudinal gradient in NW-Europe as a spatial analogue for future increases in temperature as well as nitrogen availability.

Our screening of 70 species typical of *Sphagnum*-dominated peatlands showed that leaf litters of *Sphagnum* mosses, evergreen and deciduous shrubs, graminoids and forbs differed significantly in litter chemistry (total N, P, soluble phenolics, C and lignin concentrations, and phenol/N, phenol/P, C/N, C/P, lignin/N and lignin/P ratios) and that the patterns among the growth forms were independent of the regional environmental conditions for all variables. Differences in litter chemistry among growth forms were usually larger than differences related to the environmental gradient. However, after 8 and 20 months incubation of the same litters in outdoor, *Sphagnum*-based decomposition beds, growth forms mostly differed in decomposability as well, but their ranking varied with latitude. *Sphagnum* litters decomposed slower than other litters in all regions, again explaining its high representation in organic deposits of peatlands. Forb litters generally decomposed fastest, while the differences among the other growth forms were small, particularly at higher latitudes.

Multiple regression analyses showed that growth forms were better at predicting leaf litter decomposition than chemical variables in warm-temperate peatlands with a high N-load, but less so in the sub-arctic, low-N region. Together, our results only partly supported the usefulness of a growth-form based functional classification in predicting the effects of environmental change on litter quality and decomposability. Changes in the relative abundance of growth forms in response to environmental changes may be more important than large environmental changes themselves in determining ecosystem leaf litter chemistry. However, climatic and nutritional constraints in high-latitude peatlands promote convergence towards nutrient-efficient plant traits, resulting in similar decomposition rates of vascular growth forms at different levels and combinations of litter chemistry variables.

We completed the study of the cycle of nutrients and carbon through plants and their litter in **chapter 5**, in which we investigated the consequences of differences in litter chemistry and decomposability among plant species and growth forms for new plant

growth, through the release of plant available nutrients and growth inhibitory compounds. In order to do this, we compared the short-term (9.5 months) and medium-term (21.5 months) feedback effects of different leaf litter species and growth forms (quality), and of litter quantity on plant production, and tested whether plant growth forms can be used to generalise interspecific differences.

Leaf litters of 20 sub-arctic vascular peatland species changed clearly over time in their effects on the test plant *Poa alpina*. Across all growth forms, litter reduced plant biomass after 9.5 months, by up to 49 % compared with untreated plants. This effect was strongest for litters with a high decomposition rate or low initial lignin/P ratio. In the second year, however, litter effects on biomass production were neutral or positive, which was related to initial litter N concentration (positive), and C/N, phenol/N and phenol/P ratios (negative), but not to litter decomposability. This indicated that fast initial decay enhanced microbial or chemical nutrient immobilisation and phytotoxicity by phenolic or other carbon compounds, but that nutrient mineralisation was stimulated in a later phase.

The differences in the effect size among several litter species were large; e.g. plant biomass increase was up to 55 % reduced by *Arctostaphylos alpinus* litter compared with *Saussurea alpina* litter. Differences in response to increasing litter quantities (100, 200 or 300 g m^{-2}) were smaller than or of similar magnitude as differences in response to three contrasting litter species. Growth forms did not differ in litter effects in the first year, but second-year plant production tended ($P < 0.10$) to increase in response to litters of different growth forms, in the order: evergreen shrubs < graminoids or deciduous shrubs < forbs. The results of **chapter 5** thus indicated that, even within nutrient-constrained ecosystems such as northern peatlands, vascular plant species and possibly growth forms may clearly differ in litter feedbacks to plant growth. However, the long-persisting negative effects of many peatland litters across all growth forms emphasised the importance of plant growth strategies with a reduced dependence on mineralised nutrients, through efficient conservation or access to alternative nutrient sources.

In the final chapter of this thesis, **chapter 6**, I addressed the general question whether plant growth-form-based functional classifications are useful in predicting plant-mediated production and decomposition feedbacks of northern peatlands to climate change. By integrating the results of the previous chapters with complementary literature, I assessed the degree to which the different groups of species in each hierarchical level of these classifications comply with three conditions, regarding their growth and production responses to climate change, and their effects on decomposition, nutrient availability and plant growth: (1) They should differ on average from each other in their responses or their effects under identical conditions. (2) They should represent less variation therein among

the species within groups than among species of different groups. And (3) they should differ consistently from each other under changing conditions.

The analysis indicated that plant species of different growth forms may differ substantially in their growth and production responses to climate change, and in their effects on decomposition and mineralisation processes (condition 1). However, the differences among the species and groups and their homogeneity may depend upon the environment (conditions 2 and 3). As a consequence, not all sub-divisions of the growth-form-based classification may be necessary or useful to generalise individual responses or effects. To distinguish vascular plants and (*Sphagnum*) mosses seemed to be essential for all generalisations, because their growth and production responses are often opposite, they have strong, direct mutual interactions, and because their litter decomposition strongly differs. Further sub-divisions into woody versus non-woody plants may be needed to include interspecific competition and whole-plant litter production and decomposability. The most detailed sub-division discussed in this thesis, differentiating evergreen and deciduous shrubs, forbs, and graminoids, may be useful in predicting longer-term litter feedbacks to plant growth, through the release of plant available nutrients. At almost all hierarchical levels, however, the usefulness of the sub-divisions clearly depends on our understanding of how the responses and effects of the growth forms interact with local and regional biotic and abiotic conditions, and the exact changes in climate throughout the year.

NEDERLANDSE SAMENVATTING

DE INVLOED VAN PLANTENGROEIVORMEN EN KLIMAAT OP PRODUCTIE EN AFBRAAK IN NOORDELIJKE VENEN

Noordelijke venen bedekken grote stukken land in arctische, subarctische en boreale gebieden en spelen een belangrijke rol in de koolstof balans van onze planeet. Lange tijd hebben deze noordelijke veengebieden netto koolstof opgeslagen: koolstof (C) werd er langzamer afgegeven aan de atmosfeer, door de afbraak van dode, organische weefsels, dan dat atmosferische koolstofdioxide (CO_2) werd vastgelegd door de productie van nieuwe plantenbiomassa. De kringloop van koolstof door veen-ecosystemen hangt sterk samen met de cycli van andere nutriënten, zoals stikstof (N) en fosfor (P), doordat al deze elementen betrokken zijn bij zowel de productie als de afbraak van plantenweefsels. De snelheid van beide processen wordt bovendien beheerst door de eigenschappen van de planten waaruit de vegetatie is samengesteld, zoals dominante veenmossen (*Sphagnum* spp.) in venen, en door verscheidene ongunstige abiotische omstandigheden in noordelijke venen, zoals de lage temperaturen gedurende een groot deel van het jaar, gebrek aan zuurstof en de lage toevoer van nutriënten.

Voor de komende 50-100 jaar wordt verwacht dat het klimaat in zowel de zomer als de winter op hoge noordelijke breedtegraden duidelijk zal veranderen. Deze veranderingen zullen waarschijnlijk zowel de temperatuur als de neerslag betreffen. Dergelijke veranderingen in het klimaat kunnen direct de productie- en afbraaksnelheden in noordelijke venen beïnvloeden, maar er kunnen ook verschillende indirecte effecten zijn, via verschuivingen in de soortensamenstelling van de vegetatie. Vooral op de langere termijn kunnen zulke indirecte effecten van klimaatveranderingen via planten van belang zijn. Om over de reacties van planten op klimaatveranderingen en hun effecten op ecosysteemprocessen algemene uitspraken te doen is dus noodzakelijk, maar dit wordt bemoeilijkt door de aanzienlijke verschillen in de soortensamenstelling van de vegetaties van noordelijke venen. Daarom is een functionele indeling van planten nodig. In dit proefschrift onderzoek ik hoe klimaatveranderingen cruciale onderdelen van de koolstof kringloop van noordelijke veengebieden beïnvloeden, door veranderingen in de productie en afbraak van plantenbiomassa. In het bijzonder heb ik daarbij bestudeerd of indirecte effecten van klimaatveranderingen via de planten gegeneraliseerd kunnen worden door plantensoorten te groeperen op basis van hun groeivormen (dat wil zeggen: veenmossen, altijdgroene houtige gewassen, bladverliezende houtige gewassen, gras-achtigen en kruiden).

Het eerste deel van dit proefschrift is gewijd aan de effecten van veranderingen in zomer- en winterklimaat op de groei en productie van typische veen-plantensoorten, behorende tot verschillende plantengroeivormen. Met behulp van transparante, kunststof, open-top tenten (*OTCs*) manipuleerden we de temperatuur en sneeuwcondities op een subarctisch veen. Door verschillende combinaties te maken van aan- of afwezigheid van de tenten in verschillende seizoenen, manipuleerden we zomer-, winter- en voorjaarsklimaat onafhankelijk, en creëerden we zes verschillende klimaat regimes, welke verschillende aspecten van het verwachte toekomstige klimaat nabootsten. In **hoofdstuk 2** staan de effecten van de behandelingen op het microklimaat (temperatuur, sneeuw, vocht) beschreven. De open-top tenten verdubbelden de dikte van het sneeuwdek in de winter, waardoor de gemiddelde luchttemperatuur 0,5-2,8 °C werd verhoogd. In het voorjaar verhoogden de tenten de luchttemperatuur met 1,0 °C. Opwarming met de open-top tenten in de zomer resulteerde in een 0,9 °C hogere luchttemperatuur, terwijl er geen toename was in het dampdruk-tekort in de lucht.

Hetzelfde hoofdstuk zetten we voort met het onderzoeken van de reacties van het dominante veenmos *Sphagnum fuscum* op de experimentele klimaatveranderingen, waarbij we keken naar de lengtegroei in de zomer, de structuur van de moslaag en de biomassaproductie. De kleine, maar realistische klimaatmanipulaties hadden sterke

effecten op *S. fuscum*. Zomeropwarming verhoogde de lengtegroei met 42-62 %, terwijl de biomassadichtheid van de moslaag afnam. Als gevolg hiervan was er een trend ($P < 0,10$) voor een toename in biomassaproductie. Extra sneeuw in de winter verhoogde de biomassaproductie met 33%, hoewel de lengtegroei en biomassadichtheid niet significant veranderden. Voorjaarsopwarming, toegevoegd aan de extra sneeuw behandeling in de winter, versterkte het effect van de sneeuwbehandeling niet significant, maar het is mogelijk dat onze metingen een deel van de vroege voorjaarsgroei hebben gemist. Er waren geen significante interacties tussen de zomer- en de winter-/voorjaarsbehandelingen, hetgeen aangeeft dat de afzonderlijke effecten opgeteld kunnen worden.

De resultaten van **hoofdstuk 2** duidden erop dat een toename in de dikte van het sneeuwdek kan leiden tot een toename in de koolstofopname van noordelijke venen, aangezien dergelijke condities de biomassaproductie van *S. fuscum* stimuleerden zonder dat de structuur van het veenmos veranderde. Daarentegen kunnen hogere temperaturen in de zomer op de langere termijn mogelijk negatieve gevolgen hebben voor de productie van deze veenmossen, doordat de bijkomende veranderingen in de structuur het vochtvasthoudende en -transporterende vermogen van de moslaag kunnen verminderen. Bovendien zou de sterk toegenomen lengtegroei van *Sphagnum* de interacties met andere mossen en vaatplanten kunnen beïnvloeden.

In **hoofdstuk 3** onderzochten we deze laatste optie nader. Aangezien vaatplanten met verschillende groeivormen verschillen in hun strategieën om het hoofd te bieden aan zowel het gure klimaat en de lage nutriëntenbeschikbaarheid in noordelijke venen, als aan de voortdurend toenemende hoogte van de veenmoslaag waarin ze groeien, kunnen ze op verschillende manieren beïnvloed worden door klimaatveranderingen. Klimaatveranderingen kunnen daarbij zowel directe effecten hebben, als indirecte effecten via veranderingen in de groeisnelheid van de veenmossen. We onderzochten daarom deze directe en indirecte effecten van onze manipulaties in het zomer, winter- en voorjaarsklimaat op vier soorten van contrasterende vaatplanten-groeivormen (een altijdgroene struik, een bladverliezende struik, een gras en een kruid). We keken daarbij naar de biomassa- en stikstofverliezen via de productie van bladstrooisel voor alle vier de soorten, en naar de lengtegroei van de twee struikjes.

De directe en indirecte effecten van zomeropwarming verschilden tussen de groeivormen. Toegenomen overgroei van bladeren door *Sphagnum*, ten gevolge van de zomeropwarming, stimuleerde aanvankelijk de bladverliezen als strooisel bij het kleine, altijdgroene struikje *Empetrum nigrum*. Door veranderingen in de morfologie van de hoofdtak, gerelateerd aan een marginale toename in lengtegroei, werden echter langdurige effecten op *Empetrum* voorkomen. Een duidelijkere toename in de lengtegroei van de bladverliezende struik *Betula nana* in reactie op zomeropwarming verminderde direct

de totale bladstrooiselmassa, N-concentratie en N-verliezen. Door deze veranderingen in investeringspatroon werden indirecte effecten via toegenomen overgroei van knoppen door *Sphagnum* voorkomen. Directe zomeropwarmingseffecten of indirecte effecten via toegenomen *Sphagnum*-groei op de massa, N-concentratie of N-verliezen van bladstrooisel werden niet gevonden bij het kruid *Rubus chamaemorus* en het gras *Calamagrostis lapponica*. Extra sneeuwdikte in de winter, alleen of in combinatie met voorjaarsopwarming, had geen effect op de groei van de twee struikjes, noch op de totale bladstrooiselmassa of N-dynamiek van alle groeivormen.

We concludeerden dat opwarming van het zomerklimaat waarschijnlijk de overgroei door *Sphagnum* van kleine struikjes met een beperkte groeirespons, zoals *Empetrum*, zal versterken. Bovendien kan de toegenomen lengtegroei van *Sphagnum* ervoor zorgen dat dit mos even sterk verticaal omhoog komt als sterk responsieve, maar schuin omhoog groeiende struikjes, zoals *Betula*. Dit zou een netto positief effect van zomeropwarming op de totale struikhoogte van deze soorten kunnen voorkomen, en daardoor tevens mogelijke lange termijn voordelen van een dikkere sneeuwlaag voor deze hogere struiken kunnen beperken. De productie van bladstrooisel en de daaraan gerelateerde nutriëntendynamiek worden echter waarschijnlijk sterker direct beïnvloed door opwarming via veranderingen in de bouw en investeringspatronen van de plant, dan indirect via toegenomen *Sphagnum*-groei. De verschillende reacties van de groeivormen op zomeropwarming suggereren dat zowel directe klimaateffecten als indirecte effecten via toegenomen *Sphagnum*-groei de potentie hebben om de structuur en de nutriëntendynamiek van de vaatplantengemeenschap in noordelijke venen te veranderen.

In het tweede deel van dit proefschrift heb ik me gericht op de afbraak van dode bladeren en op de vraag of indelingen van planten op basis van groeivormen (functionele classificaties) gebruikt kunnen worden om verschillen hierin tussen plantensoorten te generaliseren. Groeivormen van planten worden algemeen gebruikt om de effecten van milieuveranderingen, zoals klimaatopwarming en toegenomen N-depositie, op plantengemeenschappen te voorspellen, alsmede de consequenties van verschuivingen in soortensamenstelling voor de kringlopen van koolstof en andere nutriënten. Tot nu toe is echter onbekend gebleven in hoeverre de onderlinge rangorde van groeivormen, gebaseerd op verschillen in strooiselchemie of afbreekbaarheid, robuust is tegen veranderingen in het milieu. In **hoofdstuk 4** onderzochten we daarom of een functionele classificatie van planten gebaseerd op groeivormen een consistente voorspelling van verschillen in strooiselkwaliteit en afbreekbaarheid oplevert, onafhankelijk van de omstandigheden in de omgeving. Daarnaast onderzochten we of groeivormen net zulke goede indicatoren zijn van de afbreekbaarheid van bladstrooisel als een set van de meest gebruikte strooiselchemie

variabelen. Om deze aspecten te onderzoeken gebruikten we een grootschalige, geografische gradiënt in Noordwest-Europa, als een ruimtelijke analoog voor toekomstige toenames in temperatuur en stikstofbeschikbaarheid.

Onze screening van 70 plantensoorten die typisch zijn voor door veenmos gedomineerde venen toonde aan dat (blad)strooisels van *Sphagnum* mossen, altijdgroene en bladverliezende struiken, gras-achtigen en kruiden significant verschillen in strooiselchemie (totale concentraties N, P, oplosbare fenolen, C en lignine, en de verhoudingen van fenol/N, fenol/P, C/N, C/P, lignine/N en lignine/P), en dat de onderlinge rangordes van de groeivormen onafhankelijk waren van de regionale omgevingscondities voor al deze variabelen. De verschillen in strooiselchemie tussen de groeivormen waren doorgaans groter dan de verschillen langs de geografische gradiënt. Na 8 en 20 maanden incubatie van dezelfde strooisels in decompositiebedden op basis van veenmos, bleek dat de afbreekbaarheid van strooisels ook verschilde tussen de groeivormen, maar dat de onderlinge rangorde varieerde langs de gradiënt. Het strooisel van *Sphagnum* mossen werd het traagst afgebroken in elk van de drie gebieden, hetgeen onderstreept waarom deze mossen dominant aanwezig zijn in veenafzettingen. De bladstrooisels van kruidachtige planten werden in het algemeen het snelst afgebroken, terwijl de verschillen tussen de overige groeivormen klein waren, in het bijzonder op hogere breedtegraden.

Multiple regressie analyses toonden aan dat in warm-gematigde streken met een hoge N-depositie groeivormen betere voorspellers waren van bladstrooisel-afbraak dan chemische variabelen. Dit was echter minder duidelijk het geval in de subarctische regio met lagere N-depositie. Alles bij elkaar ondersteunden onze resultaten slechts gedeeltelijk het nut van functionele classificaties gebaseerd op groeivormen voor het voorspellen van de effecten van milieuveranderingen op strooisel kwaliteit en afbreekbaarheid. Veranderingen in mate van voorkomen van groeivormen in reactie op milieuveranderingen kunnen belangrijker zijn dan de milieuveranderingen zelf in het bepalen van de bladstrooisel-chemie op ecosysteemniveau. Daarentegen bevorderen de klimatologische beperkingen en lage nutriëntenbeschikbaarheid in venen op hoge breedtegraden waarschijnlijk het ontwikkelen van nutriëntenbesparende planteneigenschappen, resulterend in vergelijkbare afbreekbaarheid van verschillende groeivormen, ondanks verschillende gehaltes van diverse strooiselchemie variabelen.

We voltooiden de studie van de kringloop van nutriënten en koolstof door planten en hun strooisel in **hoofdstuk 5**, waar we nader onderzochten wat de consequenties zijn voor de groei van planten van de aanwezigheid van bladstrooisels van plantensoorten en groeivormen die verschillen in strooiselchemie en afbreekbaarheid, en die daardoor de afgifte van voor de plant beschikbare nutriënten alsook groeiremmende stoffen kunnen beïnvloeden. Hiertoe vergeleken we de terugkoppelingseffecten van bladstrooisels van

verschillende soorten en groeivormen (kwaliteit) en van strooiselhoeveelheid op de plantenbiomassaproductie op de korte (9,5 maanden) en langere (21,5 maanden) termijn, en testten of groeivormen gebruikt kunnen worden om de verschillen tussen de strooiselsoorten te generaliseren.

De effecten van de bladstrooisels van 20 subarctische vaatplanten op de testplant *Poa alpina* veranderden duidelijk door de tijd. Na 9,5 maanden reduceerden de bladstrooisels van alle groeivormen de massa van de testplanten ten opzichte van onbehandelde controleplanten, met een maximum reductie van 49%. Dit effect was het sterkst bij strooisels met een hoge afbreekbaarheid of een lage uitgangsverhouding van lignine/P. In het tweede jaar waren de effecten van de strooisels echter neutraal tot positief, hetgeen gerelateerd was aan de initiële N-concentratie (positief), en de verhoudingen van C/N, fenol/N en fenol/P (negatief), maar niet aan de afbreekbaarheid. Dit duidde erop dat snelle afbraak in het begin de microbiële of chemische immobilisatie van nutriënten en fytotoxiciteit van fenolen of andere koolstofverbindingen versterkte, maar dat de afgifte van nutriënten later werd gestimuleerd.

De verschillen tussen de soorten in hun effect op de plantenmassa was groot; zo reduceerde *Artostaphylos alpina* strooisel de biomassatoename in het tweede jaar met wel 55% ten opzichte van de biomassatoename bij *Saussurea alpina* strooisel. Verschillen ten gevolge van toenemende strooisel hoeveelheden (100, 200 of 300 g m^{-2}) waren kleiner dan of van vergelijkbare grootte als verschillen ten gevolge van drie contrasterende strooiselsoorten. De vier geteste vaatplant-groeivormen verschilden niet in hun strooiseleffecten in het eerste jaar, maar de plantenproductie in het tweede jaar vertoonde een trend voor een toename in de volgorde: altijdgroene struiken < gras-achtigen of bladverliezende struiken < kruiden. De resultaten van **hoofdstuk 5** wijzen er dus op dat, zelfs in door nutriënten beperkte ecosystemen zoals noordelijke venen, verschillende soorten vaatplanten en mogelijk groeivormen aanzienlijk kunnen verschillen in de terugkoppelingseffecten van hun bladstrooisel op plantengroei. De langdurig negatieve effecten van vele strooisels van venen, van alle groeivormen, benadrukt echter het belang van plantenstrategieën met een beperktere afhankelijkheid van minerale nutriënten, door deze efficiënt te conserveren of door toegang te hebben tot alternatieve nutriëntenbronnen.

In het laatste hoofdstuk van dit proefschrift, **hoofdstuk 6**, heb ik me gericht op de vraag of functionele classificaties van planten gebaseerd op groeivormen nuttig zijn bij het voorspellen van de terugkoppelingseffecten van plantenproductie en -afbraak processen in noordelijke venen naar veranderingen in het klimaat. Door de resultaten van de voorafgaande hoofdstukken te integreren met aanvullende literatuur, heb ik gepoogd vast te stellen in welke mate de verschillende groepen van soorten in elk hiërarchisch niveau van

dergelijke classificaties voldoen aan drie voorwaarden, met betrekking tot hun groei- en productieresponsen op klimaatveranderingen, en hun effecten op afbraak, en nutriënten-beschikbaarheid en plantengroei: (1) De groepen moeten gemiddeld van elkaar verschillen in hun responsen of effecten onder gelijke omstandigheden. (2) De variatie in deze responsen en effecten tussen de soorten binnen elke groep moet kleiner zijn dan tussen de soorten van verschillende groepen. En (3) de groepen moeten consistent van elkaar verschillen onder veranderende omstandigheden.

De analyse gaf aan dat plantensoorten van verschillende groeivormen aanzienlijk kunnen verschillen in hun groei- en productieresponsen op klimaat veranderingen, en in hun effecten op afbraak- en mineralisatieprocessen (1^{e} voorwaarde). Echter, zowel de verschillen tussen de soorten en groeivormen als de homogeniteit van de responsen van de soorten binnen de groeivormen kunnen variëren, afhankelijk van de omgevingscondities (2^{e} en 3^{e} voorwaarden). Het gevolg daarvan is dat niet elk niveau van onderscheid binnen een classificatie gebaseerd op groeivormen noodzakelijk of zelfs nuttig hoeft te zijn om bepaalde responsen of effecten te generaliseren. Het onderscheid tussen vaatplanten en (*Sphagnum*) mossen lijkt essentieel voor het generaliseren van elke respons of effect, aangezien hun groei- en productieresponsen vaak tegengesteld zijn, omdat ze sterke wederzijdse interacties kunnen hebben, en omdat de afbraaksnelheid van hun strooisel sterk verschilt. Verdere splitsing in houtige tegenover niet-houtige planten kan noodzakelijk zijn om de rol van competitievermogen bij productieresponsen te betrekken en bij het generaliseren van productie en afbreekbaarheid van strooisel op het niveau van de gehele plant, aangezien deze groepen daarin sterk kunnen verschillen. De meest gedetailleerde onderverdeling besproken in dit proefschrift, waarbij altijdgroene en bladverliezende struiken, kruiden en gras-achtigen worden onderscheiden, kan nuttig zijn voor het voorspellen van lange termijn terugkoppelingseffecten van strooisel op plantengroei, via de afgifte van beschikbare nutriënten. Op vrijwel elk hiërarchisch niveau geldt echter dat het nut van de onderverdeling afhangt van hoe goed we begrijpen hoe de responsen en de effecten van groeivormen worden beïnvloed door de locale en regionale biotische en abiotische condities, en door de exacte veranderingen in het klimaat door het hele jaar heen.

SVENSK SAMMANFATTNING

INVERKAN AV VÄXTFORM OCH KLIMAT PÅ PRODUKTION OCH NEDBRYTNING I NORDLIGA TORVMARKER

Översättning: Bo Wallén

Stora delar av arktiska, subarktiska och boreala områden täcks av torvmarker som spelar en avgörande roll för kolbalansen på vår jord. Torvmarker har under lång tid fungerat som kolsänkor genom att inlagringen av kol i nyproducerad biomassa har överstigit nedbrytningsförlusterna. Kolets kretslopp i torvmarker är tätt sammanknutet med andra ämnen, såsom kväve (N) och fosfor (P), genom produktionen och nedbrytningen av växtmaterial. Båda processerna styrs av de växter som dominerar vegetationen, vanligtvis vitmossor (*Sphagnum*), samt av olika ogynnsamma förhållanden, såsom låga temperaturer under merparten av året, syrebrist och låg näringstillförsel.

Under de närmaste 50-100 åren förväntas både sommar- och vinterklimatet genomgå kraftiga förändringar. Bland annat förväntas stigande temperaturer och förändrade nederbördsförhållanden. Förutom att dessa förändringar direkt påverkar produktion och nedbrytning av biomassa, förväntas de också resultera i förskjutningar i vegetationssammansättningen. Effekterna av dessa vegetationsförändringar kommer troligtvis att vara

särskilt viktiga på lång sikt. Nordliga torvmarker karakteriseras av en förhållandevis stor variation i vegetationssammansättning. För att man skall kunna generalisera effekterna av klimatförändringar behövs därför en funktionell klassificering av de ingående växtarterna. I den här avhandlingen undersöker jag effekten av klimatpåverkan på delar av kolets kretslopp i torvmarker. Jag studerar särskilt inverkan på produktion och nedbrytning. Jag undersöker i synnerhet om man genom att gruppera de ingående växterna i funktionella former (till exempel vitmossor, städsegröna ris/buskar, lövfällande ris/buskar, graminider och örter) kan dra generella slutsatser om de effekter som växterna i sig orsakar på grund av klimatförändringarna.

Den första delen av avhandlingen fokuserar på de effekter som ett förändrat sommar- respektive vinterklimat har på tillväxt och produktion hos typiska myrarter med olika växtstrategier. På en subarktisk mosse manipulerade vi både temperatur- och snöförhållanden med hjälp av försökskammare med öppet tak (*open top chambers*, 'OTC'). Genom att vi kombinerade närvaro och frånvaro av försökskammare mellan olika säsonger, skapade vi sex olika klimatregimer som skulle efterlikna framtida klimatscenarion. I **kapitel 2** beskriver vi de effekter som våra manipulationer hade på mikroklimatet. Vi skapade ett fördubblat snötäcke under vintern, som i sin tur ledde till en 0,5 – 0,8°C höjning av lufttemperaturen. Under våren ökade lufttemperaturen med 1,0°C, och under sommaren som mest med 0,9°C, medan avdunstningen inte påverkades.

Vi fortsatte sedan med att mäta effekterna av förändrade klimatförhållanden på längdtillväxt och produktion, samt på mossytans struktur hos den dominerande vitmossan *Sphagnum fuscum*. De små, men realistiska förändringarna i klimat hade en kraftig påverkan på *S. fuscum*. Uppvärmningen under sommaren ökade längdtillväxten med 42 – 62%, medan volymvikten minskade, vilket tyder på en ökande biomasseproduktion ($P < 0,10$). Med en större snömängd under vintern ökade produktionen av biomassa med 33%, trots att varken längdtillväxt eller volymvikt uppvisade några signifikanta förändringar. Uppvärmning under våren hade ingen signifikant påverkan utöver effekten av snö, men vi kan ha missat en del av den tidiga vårtillväxten. Vi fann inte heller något samband mellan vinter och vår/sommarmanipulationerna, vilket tyder på att effekterna av dessa var additiva.

Resultaten i **kapitel 2** tyder på att ett ökat snötäcke under vintern ökar kolbalansen genom att produktionen av *S. fuscum* ökar utan att strukturen påverkas. Varmare somrar kan dock påverka produktiviteten negativt genom att strukturen förändras, och därmed förmågan hos *S. fuscum* att bevara och transportera vatten. Dessutom kan en kraftig längdtillväxt påverka konkurrensförhållandena med andra mossor och kärlväxter.

I **kapitel 3** undersökte vi den roll som *Sphagnum* spelar för kärlväxterna vid en klimatförändring. Kärlväxter har utvecklat olika strategier för att möta ogynnsamma

klimatförhållanden och låg näringstillgång. De påverkas därför olika både av en klimatförändring och av en ökande tillväxt av *Sphagnum*-täcket. Därför undersökte vi både de direkta effekterna och de effekter som *Sphagnum* orsakade då vi manipulerade vår-, sommar- och vinterklimat. Undersökningarna gjordes på fyra arter som representerar fyra olika växtstrategier (städsegröna och lövfällande ris/buskar, graminider och örter). Vi undersökte biomasse- och kväveförluster via bladförnan, och också längdtillväxten hos de två risen.

Effekterna av uppvärmning under sommaren skilde sig mellan de olika växtformerna. En ökande överväxt av *Sphagnum* åstadkom ökade bladförluster hos den städsegröna *Empetrum nigrum*. Dock motverkades en mer långsiktig effekt av en något ökande längdtillväxt av skotten. Hos den lövfällande *Betula nana* minskade både bladbiomassa och N-koncentration, och därmed också kväveförlusterna. Dessa förändringar motverkade indirekt den effekt som *Sphagnum* åstadkom genom den ökade överväxten. Varken *Rubus chamaemorus* eller *Calamagrostis lapponica* påverkades med avseende på bladmassa, kvävekoncentration eller kväveförluster. Ett ökat snötäcke, med eller utan uppvärmning under våren, hade ingen påverkan vare sig på tillväxten hos ris, eller på den totala förnamängden eller N-dynamiken hos någon av de olika växtformerna.

Vi drog därför slutsatsen att uppvärmning under sommaren troligtvis ökar överväxten av lågväxande ris med begränsad tillväxtrespons såsom *Empetrum*. En ökad vertikal tillväxt gör det möjligt för *Sphagnum* att hålla jämna steg med de ris såsom *Betula*, som svarar med en tillväxtökning. Detta kan motverka effekten av sommaruppvärmning på kronhöjden, och på så sätt motverka mer långsiktiga positiva effekter av ett ökat snötäcke. Bladförnafall och näringsdynamik påverkas dock troligtvis mer direkt av uppvärmning än av tillväxtökningen hos *Sphagnum*. De olika reaktionerna på uppvärmning under sommaren tyder på att både direkta och *Sphagnum*-inducerade effekter av klimatet potentiellt kan påverka kärlväxternas samhällsstruktur och näringsdynamik.

I del två av avhandlingen behandlar jag nedbrytningen av bladförna. Jag undersöker om man genom att använda olika växtformer kan dra generella slutsatser om skillnader mellan olika arter. Växtformer används allmänt för att kunna förklara effekterna av miljöförändringar, såsom uppvärmning och ökat kvävenedfall, på växtsamhällen och de därmed förknippade effekterna av artförskjutningar på kol- och näringsflöden. Dock återstår det att fastställa hur rangordningen av växtformerna baserad på förnakemi eller nedbrytbarhet står emot en miljöförändring. I **kapitel 4** undersökte vi därför om en funktionell klassificering baserad på växtformer kunde användas för att förutsäga mönster i förnakvalité och nedbrytbarhet, oberoende av omvärldsvariabler. Vi testade också om växtformen är lika användbar som de vanligtvis använda kemiska variablerna för att förutsäga nedbrytbarhet. Vi arbetade

längs en nord-sydgradient genom NW Europa för att efterlikna en framtida ökning av både temperatur och kvävenedfall.

Vår granskning av 70 typiska torvmarksarter visade att *Sphagnum*, städsegröna och lövfällande buskar och ris, graminider och örter signifikant skilde sig åt med avseende på bladkemi (totalkväve, totalfosfor, lösliga fenoler, kol och lignin, och fenol/kväve, fenol/fosfor, kol/kväve, kol/fosfor samt lignin/fosforkvoterna). Granskningen visade också att dessa variationer mellan växtformer inte berodde på regionala skillnader i miljön. Skillnaderna i bladkemi mellan de olika växtformerna var vanligtvis större än skillnaderna längs nord-sydgradienten. Efter 8 och 20 månaders inkubationstid visade sig nedbrytbarheten hos förna skilja sig mellan de olika växtformerna, men rangordningen av växtformer baserad på nedbrytbarhet varierade längs med gradienten. *Sphagnum*förna bröts ner långsammast i alla tre regioner, vilket styrker det faktum att vitmossor är så dominerande i alla torvavlagringar. Bladförnan från örter bröts ned snabbast, medan skillnaderna mellan de andra tre växtformerna var små, speciellt på högre breddgrader.

Multipel regressionsanalys visade att växtform bättre förutspådde förnanedbrytning än kemiska variabler i myrar i varmtempererade områden med hög kvävebelastning, men var sämre på att förutsäga nedbrytbarhet i subarktiska områden med lågt kvävenedfall. Sammanfattningsvis stödde våra resultat endast delvis hypotesen om användbarheten av en växtformbaserad funktionell klassificering för att förutspå effekter av miljöförändringar på förnakvalité och nedbrytbarhet. Variationer i relativ utbredning av växtformer som svar på förändringar i miljön kan vara viktigare än kraftig miljöförändringar i sig för att reglera bladkemin på ekosystemnivå. I torvmarker på nordliga breddgrader verkar emellertid klimat och begränsningar i näringstillgång för en utveckling av näringseffektiva växtegenskaper, vilket resulterar i likartade nedbrytningsegenskaper hos olika kärlväxtformer.

Vi fullföljde studien av kretsloppen av näringsämnen och kol i **kapitel 5**, där vi undersökte hur tillväxten påverkades av pålagring av förna från växtarter och växtformer med olika förnakemi och nedbrytbarhet. Vi undersökte speciellt hur näringsämnen och tillväxthämmande substanser frigjordes. Vi jämförde effekterna av återkopplingsmekanismer mellan olika typer av bladförna och växtformer (kvalité), och förnamängder, på produktionen, både på kort (9,5 månader) och på längre (21,5 månader) sikt. Vi testade huruvida växtformer kan användas för att generalisera mellanartskillnader.

Förna från 20 kärlväxter från subarktiska torvmarker hade klart olika påverkan på vår försöksväxt *Poa alpina*. I samtliga fall åstadkom en pålagring av förna en minskning av växtbiomassan med upp till 49% efter 9,5 månader. Störst effekt hade förna med hög nedbrytbarhet och låg lignin/fosforkvot. År två hade emellertid tillförsel av förna ingen eller till och med positiv effekt. Produktiviteten var nu mer relaterad till ursprunglig kvävekoncentration (positivt), samt C/N, fenol/N, fenol/P-kvoter (negativt), men inte till

nedbrytbarhet. Detta indikerar att snabb initial nedbrytning ökade den mikrobiella och kemiska immobiliseringen av näringsämnen och fytotoxiciteten hos fenoler och andra kolprodukter, men att mineralisering av näringsämnen stimulerades i en senare fas.

De olika arternas inverkan på *Poa alpina* skilde sig åt; till exempel reducerade tillförsel av *Arctostaphylos alpina* förna biomasseökningen med så mycket som 55% under det andra året jämfört med förna från *Saussurea alpina*. Olika förnamängd (100, 200, 300 g m^{-2}) gav mindre effekt än olikheter mellan arter. De olika växtformerna skilde sig inte åt under det första året, men däremot tenderade effekten av förnatillförsel under år två att variera mellan de olika växtformerna; städsegröna ris < graminider och lövfällande buskar < örter. Resultaten i **kapitel 5** indikerar sålunda att olika kärlväxter, och möjligtvis också växtformer klart skiljer sig åt med avseende på återkoppling mellan förna och tillväxt i näringsbegränsade ekosystem såsom torvmarker. Den långvariga negativa effekten som förna från olika växtformer har, visar på vikten av tillväxtstrategier som minskar beroendet av näringsämnen, genom effektiv hushållning, eller genom att skaffa sig tillgång till alternativa näringskällor.

I det sista kapitlet, **kapitel 6**, tog jag upp den generella frågan huruvida en funktionell klassificering baserad på växtformer kan användas för att förutspå hur återkopplingen mellan produktion och nedbrytning i torvmarker påverkas av klimatförändringar. Genom att sammanföra resultaten från de tidigare kapitlen med kompletterande litteraturuppgifter, fastställde jag till vilken grad de olika artgrupperna, i varje hierarkisk nivå av dessa klassificeringar, överensstämmer med tre förutsättningar med avseende på deras tillväxt och produktionsreaktioner till klimatförändringar, och deras påverkan på ekosystemfunktioner via nedbrytning och frigörande av näringsämnen via förnan: (1) De bör skilja sig åt under identiska förhållanden. (2) De bör uppvisa en mindre variation mellan arterna inom en grupp än mellan grupper. (3) De bör klart skilja sig åt under föränderliga förhållanden.

Analysen indikerade att arter tillhörande olika växtform markant kan skilja sig åt, med avseende på hur tillväxt och produktion svarar mot en klimatförändring, och hur de påverkar nedbrytning och mineralisering (villkor 1). En del skillnader och likheter mellan arter och artgrupper kan dock bero på miljön (villkor 2, 3). Följaktligen behöver vi inte nödvändigtvis alla växtformbaserade uppdelningar för att kunna generalisera individuella reaktioner. Att skilja mellan kärlväxter och vitmossor verkar dock vara grundläggande för alla generaliseringar, eftersom deras tillväxt och produktion svarar helt olika, och för att deras nedbrytbarhet starkt skiljer sig åt. En vidare uppdelning i vedartade respektive icke-vedartade växter behövs för att kunna inkludera konkurrens mellan arter med avseende på produktion och nedbrytning. Den mest detaljerade uppdelningen som diskuteras i den här avhandlingen, den som skiljer på städsegröna och lövfällande ris/buskar från örter

och graminider, kan vara användbar för att förutspå de långtidseffekter som förna har på tillväxt genom att mineralnäringsämnen frigörs. På nästan varje hierarkisk nivå är dock nyttan av en uppdelning beroende av vår förståelse för hur de olika växtformerna svarar mot lokala och regionala, biotiska och abiotiska faktorer, samt av kunskapen om de exakta klimatvariationerna under året.

TUSEN TACK!

That writing a PhD-thesis is often lonely doesn't need to be said to those who have done it before. Now that I have (almost) finished even the last remaining bits and pieces, it is, however, time to remember that there were in fact many hands and heads that have helped me to get this far. Some of you have contributed mental or practical guidance and assistance during the scientific processes, and others have offered their moral support when the work was (not yet) finished. Tusen tack till er alla!

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CURRICULUM VITAE

Ellen Dorrepaal was born in Woubrugge, the Netherlands, on 10 May 1974. After graduating from secondary school at the Barlaeus Gymnasium in Amsterdam in 1992, she first studied Molecular Sciences at Wageningen University for one year, and then changed to Biology at Utrecht University. During her M.Sc., she investigated the role of fructans in protecting membranes in relation to drought stress in plants (Department of Molecular Plant Physiology), the role of positive plant interactions in stabilising frost soils in the sub-arctic (Department of Plant Ecology and Sheffield Centre for Arctic Ecology), and the effects of N-deposition on the moss layer of Dutch fens (Department of Landscape Ecology). Parallel to this, she was a board member of the Utrecht Biologist Society (students association), and the student-member of the board of the Faculty of Biology. She graduated in November 1999 *cum laude* for her M.Sc. in Biology. In January 2000 she started her Ph.D. research at the Department of Systems Ecology, Vrije Universiteit Amsterdam, the results of which are presented in this thesis. Since February 2005, she has continued her research in the same Department as a postdoctoral researcher, focussing on the effects of climate change on the carbon dynamics of deeper peat layers in sub-arctic peatlands.

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Dorrepaal, E., Aerts, R., Cornelissen, J.H.C., Callaghan, T.V. and Van Logtestijn, R.S.P. (2003) Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. *Global Change Biology* 10: 93-104.

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Dorrepaal, E., Cornelissen, J.H.C. and Aerts, R. Changing leaf litter feedbacks on plant production across contrasting sub-arctic peatland growth forms. (Submitted)

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